

A REVIEW OF THE GENUS *ANOTYLUS* C. G. THOMSON (COLEOPTERA : STAPHYLINIDAE)

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SYNOPSIS

The genus *Anotylus* C. G. Thomson, containing 350 species here regarded as valid, is re-defined. Morphological variation within the genus is briefly reviewed. A summary of available data concerning zoogeography, biology, immature stages and fossil species is provided. Subcosmopolitan and adventive species are individually but briefly discussed. Sixty-five specific names are newly assigned to *Anotylus*, fourteen of them in synonymy. Seven new generic synonymies and thirty new specific synonymies are noted.

INTRODUCTION

THE present account stems from studies of the taxonomy and phylogeny of the Oxytelini on a world basis. The introductory sections of this paper are longer and more discursive than is usual for a taxonomic account of limited scope, for the following reasons. Firstly, I consider it useful for a taxonomist to provide some indication of the possible value of his chosen studies and, in the case of taxonomic work on Coleoptera at the species-level, important to justify his choice, with due regard to the time and effort involved. Secondly, users are better able to evaluate a taxonomic work if its procedural and philosophical basis has been stated. In particular, I feel that the user is entitled to fairly explicit information

concerning the *nature* of a classification which is newly proposed, and concerning aspects of procedure which greatly influence the precision of results. Thirdly, as far as aims, procedure and philosophical basis are concerned, parts of the present work may be regarded as a common introduction to projected accounts of other oxyteline genera as well as to further papers on the genus *Anotylus* (e.g. Hammond, in press).

At least some work at the species-level is essential if the systematist is not to deprive himself of a wide range of useful experience. The Oxytelini commend themselves, at the present time, to this type of study for a variety of reasons. Favourable personal circumstances include ready availability of much of the relevant type-material. The generic and supra-generic classification of the subfamily Oxytelinae has recently been competently revised (Herman, 1970). Improvements to this classification are most likely to stem from comprehensive studies of species. However, in both taxonomic and other respects, the great majority of species are, at present, poorly known. More than 50% of Oxytelini have received no published mention, apart from catalogue listings, since their original description. Probably less than 10% of described species can be satisfactorily identified by means of existing keys and diagnoses. Large numbers of species await description. The Oxytelini are a large and successful group, frequently well represented in collections made for systematic or applied purposes. In certain situations species of Oxytelini may form a considerable part of the insect biomass. This is particularly reflected in samples of insects taken in flight or attracted to light-traps. Any poorly known but successful group of organisms whose members are frequently common in samples taken for ecological purposes may be considered to merit the attention of taxonomists. If, as seems likely, but unlike most Staphylinidae, species of Oxytelini feed largely on dead plant material, then it may be useful to know more of their ecology and therefore of their taxonomy. Species of this group may prove to be of some importance in the decomposition of plant matter, including the dung of herbivores. A wide range of speciation patterns appears to be exhibited by species of Oxytelini. A variety of reproductive isolating mechanisms may frequently be detected within a single genus or species-group. Taxonomic studies involving the collation of morphological, distributional and ecological data will enable more effective comparisons of those situations where reproductive isolation appears to have been achieved as a result of extrinsic factors, and those where intrinsic factors are likely to have been essential ingredients in speciation processes.

I feel that the results of studies on the Oxytelini are most appropriately presented, where practicable, in terms of the component genera and monophyletic groups of species within the genera. The present paper is intended to provide an introduction to the genus *Anotylus* Thomson, as defined here undoubtedly the largest genus of Oxytelini. An account of the taxonomy and a discussion of the phylogeny of the *crassicornis*-group, which is considered to be monophyletic has already been prepared (Hammond, in press). Similar accounts are planned to cover other species-groups of *Anotylus* and other genera of Oxytelini. As *Anotylus* is a large but poorly understood genus, in which many species remain to be described, I have not considered it appropriate to attempt a comprehensive classification of

component species-groups at this stage. When all available material has been revised or reviewed, such a classification may be attempted and, if necessary, new generic limits proposed. A fuller discussion of zoogeography and phylogeny will also then be feasible.

As many species-groups within the genera of Oxytelini are distributed in more than one zoogeographical region, taxonomic accounts based on these groups will not necessarily fulfil practical identification needs. For this reason a series of short papers is planned, each of which is intended to enable the identification of the species of Oxytelini to be found within a particular geographical area. Such papers (e.g. Hammond, 1975*a*) are projected only where the area in question is faunistically or otherwise well delimited, and the fauna is considered to be relatively well known.

In the course of studies relevant to the taxonomy of *Anotylus* some tens of thousands of specimens of this genus, as well as at least an equal number of specimens of other genera of Oxytelini, have been examined. Most of this material consists of adults mounted on card rectangles or points and, in most cases, only exoskeletal features have been investigated. Following dissection small and fragile structures, such as genitalia, were examined in glycerine and later generally stored in micro-vials (containing glycerine), pinned beneath the specimen. A Cambridge 'Stereoscan' electron microscope was used to examine surface features at high magnifications, and also for recording purposes (Pls 1-3). Terminology generally follows that of Blackwelder (1936) or Herman (1970).

CRITERIA FOR SPECIES AND SUPRASPECIFIC TAXA

The species definition provided by Mayr (1969), that species are 'groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups' is followed here. However, such a definition still leaves room for discussion regarding status in certain special cases. It should also be noted that data are frequently inadequate to establish the status of populations studied; in such cases a classification entirely in accordance with Mayr's definition may not be achieved.

For most Oxytelini no direct information concerning reproductive isolation between allopatric populations is available, and the limits of the populations themselves are generally unknown. As information concerning ecology and biology is also extremely sparse, the principal sources from which inferences concerning presence or absence of reproductive isolation may be derived are adult morphology and, to a lesser extent, chorology. However, where sufficient study material and sufficient distributional data are available, sympatric species present relatively few problems. Sister-species of Oxytelini are frequently sympatric and exhibit marked differences in male secondary sexual structures and parts of the male genitalia. In many cases, involvement of these structures as species-specific recognition devices appears likely. Such differences may thus have contributed to successful reproductive isolation rather than have been achieved as a consequence. In this situation, examination of very few males is sufficient to make confident

inferences concerning the status of sympatric populations. For allopatric populations, of course, conclusions are much more dependent on the quality of data available concerning distribution and morphological variation within the populations.

In practical terms my treatment of allopatric forms is generally that of a 'lumper'. Where evidence concerning the nature of geographical variation is at all inconclusive, I regard samples from largely similar allopatric populations as conspecific. This does not imply any particular theoretical standpoint regarding the likelihood of reproductive isolation between such populations. I feel merely that a conservative attitude to the formal naming of taxa is appropriate in situations of uncertainty. It may also be felt that the definition of 'macro-species' and discussion of their interrelationships are the prime tasks of broad revisional studies of the members of staphylinid genera at the present time. However, any morphological differences which appear to be exhibited by allopatric components of a 'macro-species' will be noted and possibilities of reproductive isolation between them discussed.

I recognize the value of naming subspecies, in certain instances, even where direct evidence concerning gene-flow between populations is unavailable. However, I feel that the need for formal naming at this level is slight in the case of most Oxytelini. Where subunits of species appear to be recognizable their geographical and morphological features will be noted, but only where good evidence concerning the nature of the interface between subunits is available, and a practical advantage justifies the action, will subspecies be formally named. In certain cases my use of subspecies may also be an expression of uncertainty in relation to allopatric forms which, on the basis of further evidence, may prove to be distinct species.

I agree with Whitehead (1972) that in studies of single genera 'the existing concept of the genus should be accepted unless it is poorly defined or clearly unreasonable'. I therefore accept *Anotylus*, much as defined by the most recent revisor of genera of Oxytelinae (Herman, 1970), as a group of generic rank. Although subgenera are not employed in the present work I consider formal categories of infra-generic rank to be useful in the case of certain large genera. When monophyletic groups of species have been more widely recognized within *Anotylus*, and their phyletic relationships assessed, it may prove appropriate to employ formal subgeneric (or generic) names for groupings subordinate to *Anotylus*, as presently defined.

I accept the principle that a supra-specific taxon should be strictly monophyletic, and the present work attempts consistently to employ cladistic relationships as the basis of classification. Recency of common ancestry, using monophyly in the sense of Hennig (1966), is the basis of my classificatory decisions. However, I agree with Anderson (1974) that acceptance of the principles of the Hennigian approach does not mean that cladistic hypotheses can always be made with confidence. Nevertheless, the only compromises with the phylogenetic method which I wish to make are generally of a practical nature, not ones of principle, as little methodological compromise is possible without disruption of the method's logic. As pointed out by Cracraft (1974), any acceptance of patristic relationships will decrease the information content of a classification. I do not recognize the practical value of accepting paraphyletic groupings as frequently as advised by some workers who adopt a partially cladistic approach (e.g. Whitehead, 1972).

The inclusion relationships arrived at by means of hypotheses concerning the relative recency of common ancestry of taxa are unidirectional. However, in many instances, the possibility of justifying even the approximate equivalence of all taxa of the same rank is slight. For example, insufficient direct or contextual evidence is presently available for such equivalences to be estimated in the Oxytelini. For this reason the formal equivalence in rank of certain taxa will rest on arbitrary criteria. I agree with Noonan (1973) that, because of extinctions, the number of successive branching points in any lineage is generally unable to provide any absolute time scale. Equally, no absolute measure of rates of 'divergence' is available. Equivalence of age is not implied for branching points at the same level in the time axis of cladograms which I present. Although I agree that dichotomous cleavage cannot be regarded as a universal component of all speciation processes, I regard the expression of phylogenetic hypotheses in terms of dichotomies as unexceptionable, especially when reconstructions are made on the basis of the extant fauna only.

My reasons for adopting the 'Hennigian' approach stem from the conviction that systematic studies should attempt to provide hypotheses of service to biological science as a whole. Hypotheses which convey the maximum information concerning the evolutionary events which have led to the range of organisms extant at any given time are those best suited to this end. This point has been well argued by Crowson (1970). As a detailed justification of the value of the phylogenetic approach to classification I find that of Griffiths (1972) the most complete and satisfying. Some additional pertinent points are made by Cracraft (1974). The value of phenetic systems of classification lies in presenting the results of morphological or other research in a convenient manner, but I agree with Griffiths (*loc. cit.*) and Cracraft (*loc. cit.*) that the use of the Linnaean hierarchy for this purpose is ultimately unfortunate. Finally, I concur again with Griffiths (*loc. cit.*) that 'static presentations of the distribution of functional-morphological types should be regarded as special purpose [classificatory] systems', and that 'the phylogenetic system is a general-purpose classification widely useful in many branches of biology, and . . . is the most suitable classification for representation through the Linnaean hierarchy'.

TYPES

Although many different authors, some 95 in all, have contributed descriptions of new species which are today included in the Oxytelini, almost all type-material is, fortunately, extant. Most of this is available for study and I have examined primary type-material relating to about 80% of the relevant names. The evaluation of most type-material of Oxytelini presents few problems. However, individual judgements frequently need to be made regarding the precise composition of type-series. The majority of authors, including four – M. Bernhauer, M. Cameron, A. Fauvel and D. Sharp – who are responsible for some three-quarters of the names currently included in *Anotylus*, did not consistently label all specimens on which new species were based. Syntypes of some species, especially those of Bernhauer

and Cameron, have been widely distributed and are to be found in many collections. In certain cases more than one, sometimes several, 'types' of the same species, notably those of Bernhauer and Wendeler, are to be found in different collections. The recognition and evaluation of type-material of species described by J. Stephens and T. Marsham (both collections in BMNH) has been discussed by Hammond (1972). Data enabling satisfactory recognition of syntypical material described by T. Wollaston, compiled by members of the BMNH staff, is to be found in association with the principal Wollaston collection (BMNH); many of the significant points from these notes have been summarized by Johnson (1970).

Type-material of some species included in the present study has not been available for examination. The collection of Eichelbaum (formerly in Zoologisches Museum, Hamburg) is known to have been destroyed by war damage. Some of the species described by that author (1913) from East Africa are probably to be regarded as *nomina dubia* although, in some instances, apparently syntypical material is to be found in other collections. No type-material of species described by Gistel (1857) is known to exist. Much of the type-material of species described by Fauvel and deposited in the Museo Civico di Storia Naturale, Genoa has not been located. Syntypes of some of these species were retained by Fauvel in his own collection (now in the Institut Royal des Sciences Naturelles de Belgique, Brussels) but remaining syntypes of these species and several unique holotypes could not be found in the Genoa Museum in 1973 (E. Tortonese, personal communication) or 1975 (M. C. Day, personal communication). Despite several requests, material from the important collection of Professor O. Scheerpeltz (Vienna), containing types of species described by Luze as well as the holotypes of many of Scheerpeltz's own species, has not been made available for examination. Requests for loan of type-material of species described by Abdullah & Qadri (Karachi University) have also met with no response.

Lectotypes

A strict interpretation, similar to that of Hayek (1973 : 9), of Article 73 of the *International Code of Zoological Nomenclature*, is followed here. As a result the majority of species included in *Anotylus* are considered to be represented by syntypes. Where taxa are comprehensively revised, as in the case of the *crassicornis*-group (Hammond, in press), lectotypes will generally be designated. Where species are otherwise discussed (e.g. nomenclatural and synonymic notes below) I have refrained from designation of lectotypes. To quote from the *Code*, types afford 'the standard of reference that determines the *application* of a scientific name' (my italics). Unless accompanied by appropriate taxonomic evaluation of types and of the taxon to which they relate, restriction of this standard of reference would appear to be an exercise without taxonomic value.

Except where a clear indication to the contrary regarding ownership exists, lectotypes will be designated from material in museums which house the major part of the relevant author's collection. For the most prolific authors these are: Bernhauer (Field Museum of Natural History, Chicago); Cameron (BMNH); Fauvel (Institut Royal des Sciences Naturelles de Belgique, Brussels).

Nomina nuda

A number of 'manuscript-names' are to be found attached to specimens of *Anotylus* in museum collections. Many such names are the work of Bernhauer and 'types' of his 'manuscript-species' are to be found in many collections. Bierig, Cameron and Fagel also appended a number of these names to specimens in various collections. As some of these names have achieved a certain currency and have sometimes been referred to in published works they are noted where appropriate under the relevant species.

ANOTYLUS Thomson

- Anotylus* Thomson, 1859 : 44. Type-species: *Oxytelus sculpturatus* Gravenhorst, by original designation and monotypy.
- Styloxys* Des Gozis, 1886 : 15 [as subgenus of *Oxytelus* Gravenhorst]. Type-species: *Staphylinus rugosus* Fabricius, by virtual monotypy.
- Oxytelodes* Bernhauer, 1908 : 290. Type-species: *Oxytelodes holdhausi* Bernhauer, by monotypy.
- Styloxis* Des Gozis; Eichelbaun, 1909 : 119. [Incorrect subsequent spelling of *Styloxys* Des Gozis.]
- Emopotylus* Bernhauer, 1910 : 359 [as subgenus of *Oxytelus* Gravenhorst]. Type-species: *Oxytelus cuernavacanus* Bernhauer, by monotypy.
- Onotylus* Thomson; Bernhauer, 1915 : 100. [Incorrect subsequent spelling of *Anotylus* Thomson.]
- Boettcherinus* Bernhauer, 1936a : 82 [as subgenus of *Oxytelus* Gravenhorst]. Type-species: *Oxytelus planaticollis* Bernhauer, by subsequent designation (Steel, 1948 : 188).
- Oncoparia* Bernhauer, 1936b : 214. Type-species: *Oncoparia parasita* Bernhauer, by monotypy.
- Syn. n.**
- Anotylus* Thomson; Bernhauer, 1938 : 22. [Incorrect subsequent spelling of *Anotylus* Thomson.]
- Paracaccoporus* Steel, 1948 : 188 [as subgenus of *Oxytelus* Gravenhorst]. Type-species: *Oxytelus ocularis* Fauvel, by original designation.
- Boettcherianus* Bernhauer; Steel, 1948 : 188. [Incorrect subsequent spelling of *Boettcherinus* Bernhauer.]
- Oxytelosus* Cameron, 1950b : 92. Type-species: *Oxytelus abnormalis* Cameron, by virtual monotypy.
- Styloxys* Des Gozis; Fagel, 1956 : 271 (in part).
- Microxytelus* Fagel, 1956 : 272. Type-species: *Oxytelus nitidifrons* Wollaston, by original designation and monotypy.
- Anotylus* Thomson; Fagel, 1956 : 273.
- Oxytelops* Fagel, 1956 : 273. Type-species: *Staphylinus tetracarvinatus* Block, by original designation and monotypy.
- Oxytelosus* Cameron; Fagel, 1956 : 274.
- Pseudodelopsis* Fagel, 1957 : 3. Type-species: *Pseudodelopsis scotti* Fagel, by original designation.
- Anotylops* Fagel, 1957 : 8. Type-species: *Anotylops seydeli* Fagel, by original designation and monotypy. **Syn. n.**
- Oncoparia* Bernhauer; Fagel, 1965 : 338.
- Anothylus* Thomson; Coiffait & Saiz, 1968 : 420. [Incorrect subsequent spelling of *Anotylus* Thomson.]
- Metoxytelus* Coiffait & Saiz, 1968 : 422. Type-species: *Oxytelus sulcicollis* Gemminger & Harold, by original designation and monotypy. **Syn. n.**
- Anotylus* Thomson; Herman, 1970 : 414.
- Oncoparia* Bernhauer; Herman, 1970 : 421.

Anotylops Fagel; Herman, 1970 : 423.

Pseudopyctocraerus Abdullah & Qadri, 1970 : 125 [as subgenus of *Platystethus* Mannerheim].

Type-species: *Platystethus mahmoodi* Abdullah & Qadri, by original designation. **Syn. n.**

Pseudopyctocraerus Abdullah & Qadri; Abdullah & Qadri, 1970 : 125. [Incorrect subsequent spelling of *Pseudopyctocraerus* Abdullah & Qadri.]

Neopyctocraerus Abdullah & Qadri, 1970 : 126. Type-species: *Neopyctocraerus shafqati* Abdullah & Qadri, by original designation and monotypy. **Syn. n.**

Neoplatystethus Abdullah & Qadri, 1970 : 127. Type-species: *Neoplatystethus hameedi* Abdullah & Qadri, by original designation and monotypy. **Syn. n.**

Pseudoplatystethus Abdullah & Qadri, 1970 : 129 [as subgenus of *Neoplatystethus* Abdullah & Qadri]. Type-species: *Neoplatystethus meccii* Abdullah & Qadri, by original designation and monotypy. **Syn. n.**

The later citation of *Oxytelus nitidulus* Gravenhorst as type-species of *Anotylops* by Blackwelder (1943 : 91) cannot be accepted as *O. nitidulus* was not originally included. I find myself in agreement with all of Blackwelder's (1952) conclusions regarding the type-species of genera erected prior to 1950, and listed in the synonymy above. Herman (1970 : 414) discusses the fixation of a type-species for *Oxytelosus* Cameron; I agree with his conclusions. However, the type-species of *Boettcherinus* was fixed as *Oxytelus planaticollis* Bernhauer by Steel (1948 : 188) and Blackwelder's designation (1952 : 79), fortunately of the same species, is redundant.

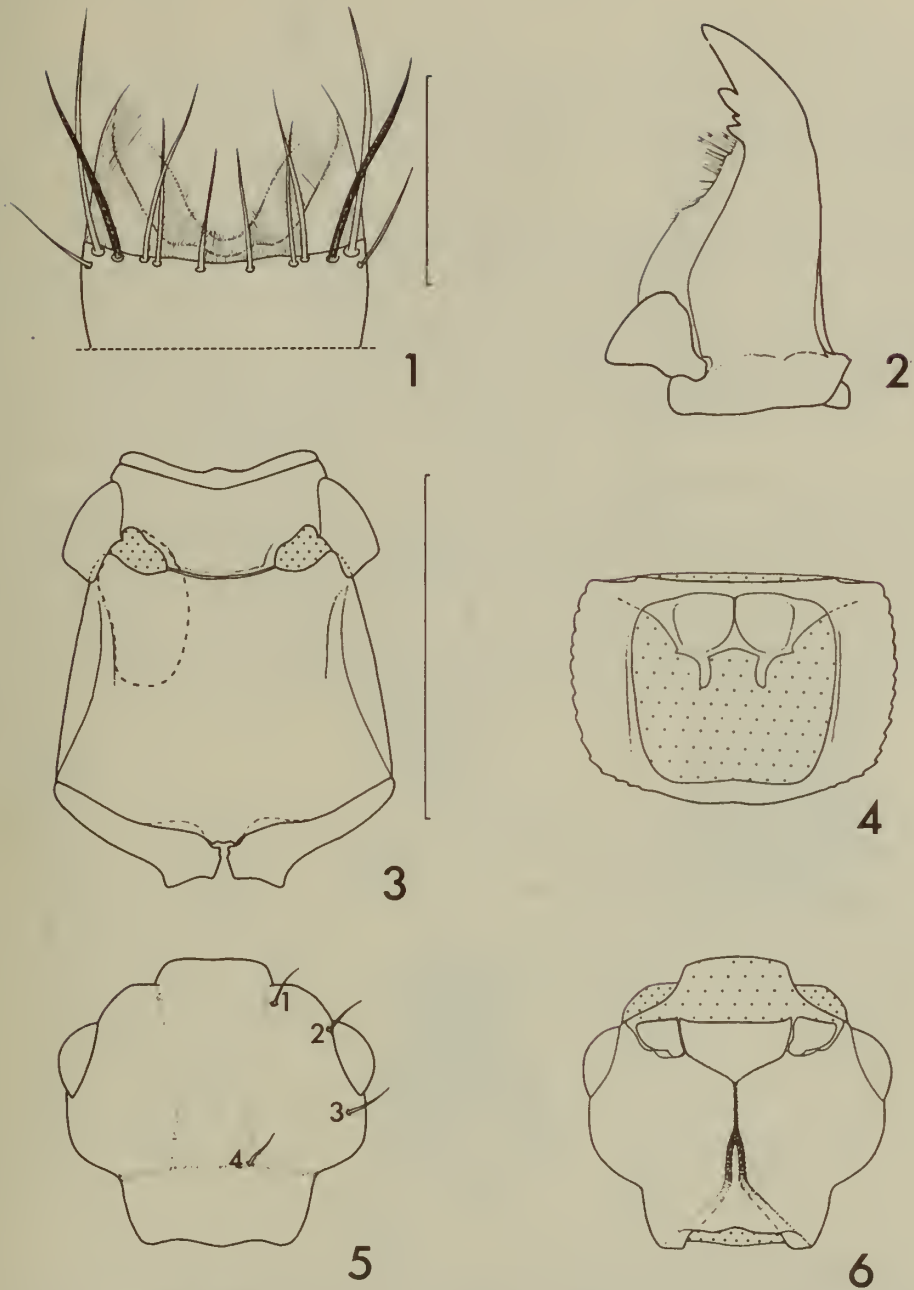
With the characters of Oxytelinae (see Herman, 1970 : 358-360). Length 1.0-7.5 mm. Form moderately broad to narrow, moderately depressed. Surface scarcely to strongly sculptured; pubescence generally inconspicuous.

Clypeus reduced, anterior margin of variable form, clypeal area distinctly or poorly delimited by epistomal groove; supra-antennal prominence generally well developed; gular sutures confluent anteriorly, then sharply divergent and parallel from middle to anterior region of neck, then sharply and continuously divergent to base of neck (Text-fig. 6); base of head constricted to form well-defined neck, vertex frequently demarcated from dorsum of neck by occipital groove (Text-fig. 5). Labrum with anterior margin more or less truncate to broadly emarginate, without median longitudinal suture (Text-fig. 1); mandibles generally with denticulate mesial edge (Text-fig. 2); antenna generally with short, moderately close to close pubescence on at least segments 6 to 11, with some long, tactile setae on all segments; segment 1 of antenna generally the longest, *constricted at base and incrassate apically*; segment 4 of maxillary palpus generally subulate (Pl. 1, fig. 28), narrower than segment 3.

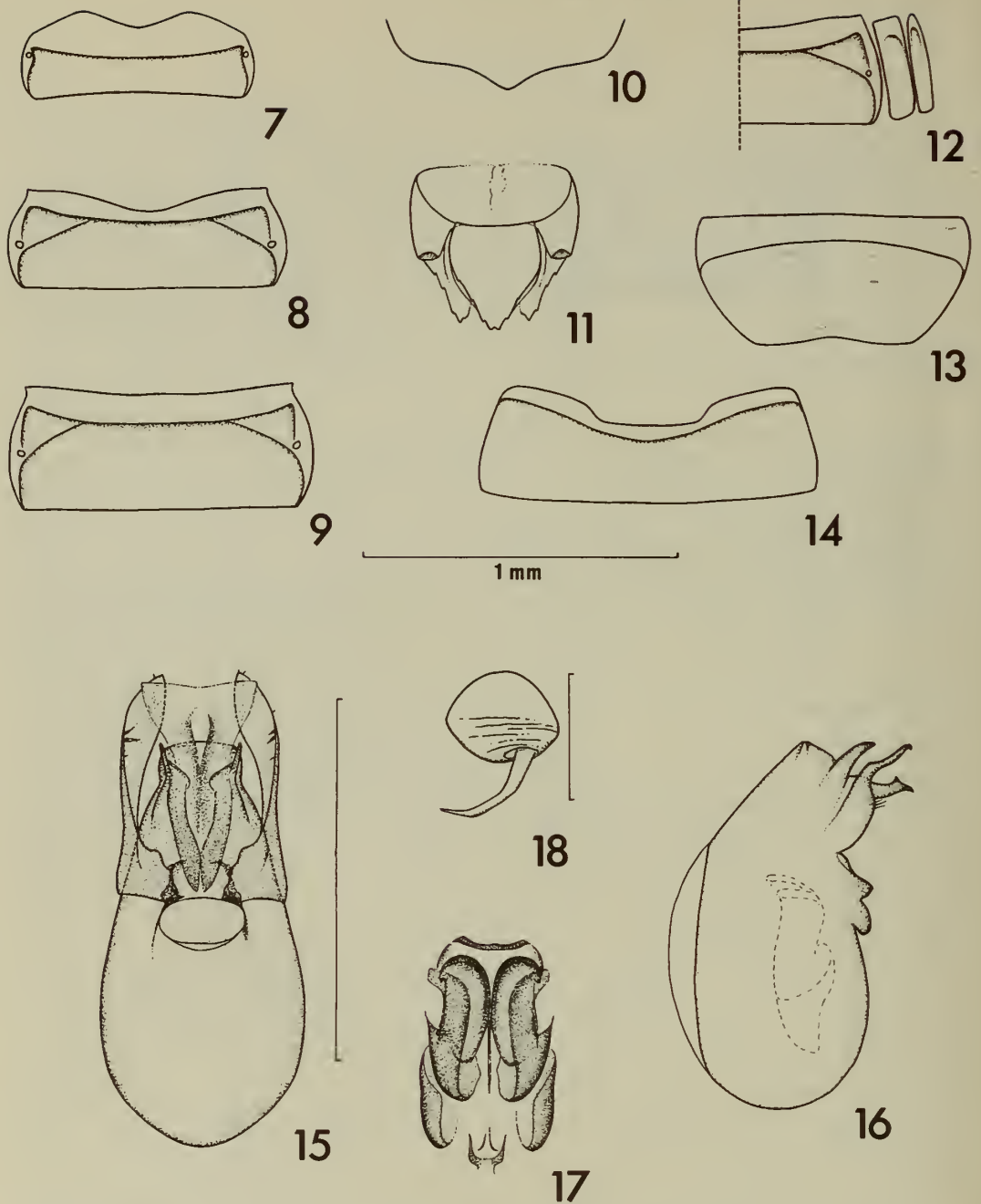
Pronotum transverse; lateral marginal bead present; dorsum generally *with three longitudinal grooves or furrows* on disc; protergosternal suture absent (Text-fig. 4); procoxal fissure absent, protrochantin concealed (Text-fig. 4); postprocoxal lobe absent, prohypomeron generally strongly deflexed and broad (Text-fig. 4); prosternal process short, carinate (Text-fig. 4). Surface of scutellum *with a trilobed impression* (Pl. 2, figs 35-37) (obsolete in *A. leleupi* (Fagel) and *A. parasitus* (Bernhauer)). Elytra transverse to very transverse, generally *not overlapping at suture*. Mesosternal process short, broad, truncate (Text-fig. 3); mesocoxae fairly widely to widely separated (Text-fig. 3) or, occasionally, more or less contiguous (*A. leleupi* and *A. parasitus* only).

Legs fairly short to short; tibiae generally with rows of spines and spinules; pro- and mesotibia generally with some fairly stout spines (Pl. 3, figs 29, 30); protibia frequently with constriction in outer third (Pl. 3, fig. 30); tarsal formula 3 - 3 - 3; first and second tarsomeres frequently of approximately equal length, together generally shorter than third; first and second tarsomeres generally with a few ventral setae flattened and blade-like.

Tergum of 2nd abdominal segment *without basolateral ridge* (Text-fig. 7); terga of 3rd to 7th abdominal segments *with basolateral ridges* (Text-figs 8, 9, 12); 2nd to 7th abdominal segments each with a pair of laterosternites on each side; paratergite and parasternite of most segments



FIGS 1-6. *Anotylus stanleyi* (Cameron). (1) Labrum, scale = 0.3 mm; (2) right mandible, same scale as 1; (3) pterothorax in ventral view; the approximate position occupied by the right mesocoxa, when in place, is indicated by the dashed line, scale = 1.0 mm; (4) prothorax in ventral view, same scale as 3; (5) head in dorsal view (appendages removed), same scale as 3; (6) head in ventral view (all mouthparts removed), same scale as 3. Large stippling in figs 3, 4 and 6 denotes the inner surface of an exoskeletal feature.



FIGS 7-18. *Anotylus stanleyi* (Cameron). (7) Tergite of 2nd abdominal segment; (8) tergite of 3rd abdominal segment; (9) tergite of 6th abdominal segment; (10) posterior margin of sternite of 8th abdominal segment in ♀; (11) terga of 9th and 10th abdominal segments of ♀ in dorsal view; (12) right half of tergite and right laterosternites of 4th abdominal segment; (13) sternite of 8th abdominal segment in ♂; (14) sternite of 2nd abdominal segment; figs 7-14 all to same scale; (15) ♂ genitalia in ventral view, scale = 0.5 mm; (16) median lobe of ♂ genitalia in lateral view; the position occupied by the internal sclerotized parts is indicated by a dashed line, same scale as 15; (17) internal sclerotized parts of median lobe of ♂ genitalia in ventral view, same scale as 15; (18) spermatheca, scale = 0.1 mm.

frequently of approximately equal breadth (Text-fig. 12), parasternite of 7th segment very narrow; sternite of 2nd abdominal segment well developed, anterior margin as in Text-fig. 14; intersegmental membranes between 2nd to 7th segments with fine, generally weak, sometimes scarcely detectable surface pattern; tergum of 9th abdominal segment frequently divided by 10th tergum; external openings of abdominal glands in tergum of 9th abdominal segment (Text-fig. 11).

♂. Head and pronotum frequently broader than in ♀, sometimes with pronounced secondary sexual modifications of these parts. Abdominal sclerites generally with few outstanding sexual modifications; posterior margin of sternite of 8th abdominal segment generally of *simple bisinuate form* (e.g. Hammond, 1975a: figs 59, 60) or more or less truncate (Text-fig. 13); median lobe of ♂ genitalia not very extensively sclerotized, elongate-oval or somewhat egg-shaped (Text-fig. 15), *lacking stout medio-ventral projections*, apico-ventral projections generally slender; internal armature of median lobe weakly to moderately well sclerotized; lateral lobes of genitalia often rather weakly sclerotized, generally of simple form (e.g. Text-fig. 15).

♀. Sternite of 8th abdominal segment with posterior margin of simple form (Text-fig. 10). Spermatheca small, form generally much as in Text-fig. 18.

The generic description given here is fairly brief as modification of generic limits in this area is a likely outcome of ongoing studies of the Oxytelini. A fairly comprehensive definition of *Anotylus*, largely as understood here, has recently been provided by Herman (1970). Characteristics in italics in the description of *Anotylus* above are those which most readily distinguish members of the genus from other Oxytelini. However, most species of *Oxytelopsis* Fauvel and *Rimba* Herman and some species of *Apocellus* Erichson are to be distinguished from species of *Anotylus* only with difficulty.

HISTORY

The concept represented in the present work by *Anotylus* Thomson has only a short history. *Anotylus* was erected by Thomson (1859), for a single species from *Oxytelus*, on the basis of characteristics which are of little significance in the definition of the genus employed here. *Anotylus* has been little used as the valid name of a genus by authors subsequent to Thomson (loc. cit.), but this name and others proposed by Thompson have frequently been employed as subgenera of *Oxytelus*. Little attention was paid to the classification of the Oxytelini during the first half of the twentieth century. The many new species described during this period, principally by Bernhauer, Cameron and Fauvel, were mostly allocated to existing genera on the basis of characteristic gestalt. No attempt is made here to review critically the work of authors who described species of *Anotylus* during this period, although it should be recognized that their species descriptions and large collections now provide a most useful basis upon which modern taxonomic work can proceed. As most species here included in *Anotylus* were, until 1970, contained in *Oxytelus*, the history of the latter genus is largely the history of both. Apart from a few recent works (discussed below), the taxonomic content of work on '*Oxytelus*' during the present century is low, and a complete review would occupy several pages to little advantage. Literature, including key-works, relating to the European fauna is fairly extensive, but accounts of other regional faunas are scarce and largely out of date. Those which retain some value as key-works include that of Fauvel (1878), who provides a key to 18 Australian species now included in *Anotylus*,

Casey (1894) with 15 Nearctic species, Cameron (1928) for Sumatra, Cameron (1930a) for India, Bernhauer (1936a) with 26 species from the Philippines, Bernhauer (1939) who provides a key to 28 small Palaearctic '*Oxytelus*', all of them *Anotylus*, Blackwelder (1943) with 7 species from the West Indies, Hatch (1957) with 7 Nearctic species, and Scheerpeltz (1962) who includes 35 Palaearctic *Anotylus* in a key. However, the only regional review of *Anotylus* which may be regarded as up to date is that included by Hammond (1975a) in his account of the Oxytelini of Ceylon.

In recent years two authors (Fagel, 1956; Herman, 1970) have provided new generic classifications which involve species placed here in *Anotylus*. In the same period, some piecemeal erection of new genera, several of which are here relegated to the synonymy of *Anotylus*, has continued. The new genera and subgenera erected by Abdullah & Qadri (1970) for a selection of species collected from dung in Karachi cannot be identified with certainty from the descriptions. However, all of these new taxa appear to be based on species of *Anotylus* and I have few reservations in assigning them to the synonymy of that genus. *Anotylus* was revived as a full genus by Fagel (1956), although used in a much narrower sense than in Herman's (1970) later work or the present account. Fagel's reclassification of genera related to *Oxytelus* Gravenhorst (1956) and supplementary papers on the same theme (1957; 1965) were based principally on the faunas of the Ethiopian and western Palaearctic regions, and are avowedly phenetic in basis. Apart from a more extensive use of illustration and study of male genitalia, the work differs little in type from that of earlier authors, such as Bernhauer and Cameron. The use of 'similarity' in assessing relationships and restriction of study material to that available from certain geographical areas limits the usefulness of Fagel's work above the species level. Herman (1970 : 415-417) has already dealt critically with Fagel's classification of genera related to *Oxytelus*. As I find myself very largely in agreement with Herman in these respects, detailed comment here is unnecessary. Although certain of Fagel's genera are clearly polyphyletic (e.g. *Styloxys*) and include species from widely separated lineages, the characters employed in Fagel's classification are likely to be of some value in assessing relationships in this area. However, the characters, mostly relating to the structure and proportion of parts of antennae, maxillary palpi and legs, require more critical and comprehensive study, and character states will need redefinition. At the specific level I have generally found myself in agreement with Fagel's (1957, etc.) conclusions. Any disagreements generally relate to interpretation of genital features. Male genitalia were examined dry by Fagel and distortion of delicate structures has frequently been reflected in his highly stylized drawings.

Herman's (1970) reclassification of the genera of Oxytelinae was the first major work on Staphylinidae to employ modern phylogenetic methods, and as such is a milestone in work on this family. This work, which incorporates a number of radical proposals, is likely to form the basis of studies on the taxonomy of Oxytelinae for some time to come, and will be referred to frequently by the present writer. At the outset it should be made clear that I find myself in agreement with the greater part of Herman's conclusions. It may be noted that much of this agreement

stems from quite independent consideration by Herman and myself of the classificatory problems involved. In some cases the same conclusions have been reached by different routes and by utilizing different sets of characters. Apart from questions of ranking and certain areas which Herman explicitly left unresolved, I find Herman's delimitation of taxa at the generic level largely acceptable and regard almost all as monophyletic units. However, at the tribal level and that which, if so formally named, might be the sub-tribal level in Herman's classification, I find the evidence for monophyly less compelling. My differences with Herman here largely relate to the significance attributed to variations in the structure of the prothorax and pterothorax. The distinctness of two lineages recognized by Herman within his Oxytelini, both of them containing species formerly included in *Oxytelus*, can scarcely be doubted. The distinctive characteristics of what may be termed the '*Anotylus* group' (*Anotylus*, *Oncoparia*, *Oxytelopsis*, *Rimba*, *Apocellus*) and the '*Oxytelus* group' (*Oxytelus*, *Anisopsis* Fauvel, *Anisopsidius* Fagel, *Paroxytelopsis* Cameron, *Hoplitodes* Fauvel) were also noted independently during my own studies. As differences between the two groups, especially those of the scutellum, tergite of 2nd abdominal segment and male genitalia, are so constant and striking, it is only surprising that little or no previous use had been made of these diagnostic characters. I accept Herman's conclusions regarding monophyly of the *Anotylus* group of genera, but have some doubts concerning monophyly of the *Anotylus* and *Oxytelus* groups together. I regard the scutellar impressions (Text-figs 34-37) of the two groups as quite independently evolved, and am by no means convinced that the basolateral ridges of the abdominal tergites are homologous in the two groups. The immediate sister-group of the *Anotylus* group may prove to be *Platystethus* Mannerheim, rather than the *Oxytelus* group.

Within the *Anotylus* group much further study is clearly needed before a satisfactory classification of the many included species can be achieved. As noted by Herman (1970) the genus *Anotylus* itself is presently a receptacle for any members of the *Anotylus* group which lack the apomorphic features employed to define other genera in this group. At the present time, and largely as treated here, *Anotylus* thus represents a taxonomic grouping of considerable practical value, but in need of thorough revision if relationships within the *Anotylus* group are to be clarified. I have included under *Anotylus* only one genus explicitly excluded from its synonymy by Herman (loc. cit.). The apomorphic characteristics employed by Herman (loc. cit.) to support retention of *Oncoparia* as a distinct genus all relate to the loss or reduction of parts, mostly as a concomitant to early loss of flight. Other characteristics exhibited by species of *Oncoparia*, notably those of the male genitalia, suggest that these species share uniquely derived features with species-groups presently contained within *Anotylus*.

MORPHOLOGICAL VARIATION

Even for such an extensive group, including species which occupy diverse vegetational zones and habitats, the range of morphological variation exhibited by *Anotylus* must be regarded as considerable. However, by far the greater part of this variation

involves relatively superficial features. Characters particularly useful in establishing major monophyletic groupings are not easy to identify. Relatively cryptic characters, some of which may prove of great value in assessing relationships, have not been extensively studied to date.

Very little is known of the structure of internal organs in *Anotylus*. The ovaries of five British species of the genus were studied by Welch (1964), who found that their ovariole numbers varied from 6–9 to 12. Other Oxytelinae (*Bledius* Leach, *Carpelimus* Leach, *Oxytelus*, *Platystethus*) and most other Staphylinidae examined by Welch exhibited 6 ovarioles per ovary, although the ovaries of *Oxytelus* and *Platystethus*, but not other oxyteline genera, were of the same racemose type as those of *Anotylus*. I have examined the spermatheca of several species of *Anotylus*, all of which proved to be of very similar structure, much as in Text-fig. 18. The testes of all Oxytelinae examined by R. T. Thompson (unpublished work) in the course of a survey of these organs in Staphylinidae were of very similar structure. However, in three species (*Oxytelus laqueatus* (Marsham), *Anotylus sculpturatus* (Gravenhorst) and/or *inustus* (Gravenhorst)?, *Platystethus* sp.), each testis was composed of six follicles, while in the fourth species studied, *Anotylus rugosus* (F.), twelve follicles were contained in each testis. In all four species the sub-cylindrical follicles opened directly into the long and narrow *vasa deferentia*, and two pairs of long, tubular accessory glands were present.

Use of a scanning electron microscope for the study of surface features has directed attention to several structures which have previously been largely ignored in systematic studies. The arrangement of sensory and other structures on the adoral surface of the labium has already been employed extensively by Herman (1972) in discussions of *Bledius* and related genera. The same author also illustrates *sensilla basiconica* on the apical segment of both labial (1972 : figs 321, 322, 446) and maxillary palpi (fig. 442). Very similar structures are found in *Anotylus* (e.g. Pl. 2, fig. 31), as well as various other Staphylinidae examined, and are assumed to be gustatory in function. Supposed chordotonal organs at the base of the 4th segment of the maxillary palpus (e.g. Pl. 1, fig. 27) were found to be present in all *Anotylus* so far examined. Herman (1972 : fig. 438) illustrates a similar organ in a species of *Bledius*. As I have already noted similarly situated structures of this type in many other Staphylinidae they may be of more or less general occurrence in at least this family of Coleoptera. I have seen no previously published mention of the short, stout setae, present in all *Anotylus* examined, which are located one on each side of the scutellum (e.g. Pl. 2, figs 35–37). However, as I have noted these (e.g. Text-fig. 34), and similar setae located at the base of the 2nd antennal segment (e.g. Pl. 3, figs 25, 26) in several other genera of Staphylinidae, they may also be of widespread occurrence. The form and siting of these setae suggest that they fulfil a proprioceptive function. The systematic distribution and variation of these and other structures particularly amenable to study with a scanning electron microscope requires further investigation. Many traditionally used characteristics of surface sculpture and vestiture, particularly of the upper surface of the body and the appendages, are already known to be of diagnostic value for both species and species-groups within the Oxytelini. Although many such surface

features may be profitably studied with light microscopes, a scanning electron microscope proves a useful adjunct for critical examination, and for clear and accurate illustration (e.g. Pls 1-3).

Certain morphological features exhibited by species of *Anotylus* are clearly correlated with particular habits or habitats. Parallel or convergent developments in such cases are likely to be frequent. For example, a suite of characteristics, including brachyptery, reduction of eyes, dense surface sculpture, etc., is found in many species which inhabit deep forest humus or other cryptic habitats. Although rare in other genera of Oxytelini flightlessness is of fairly common occurrence in *Anotylus* and *Oxytelopsis*. A similar facies is shared by species of several disparate groups of these two genera in which loss of flight has been followed by extensive changes in structure of the thorax and abdominal base, and reduction of the elytra, as well as of the flight wings. Modifications associated with loss of flight are particularly striking in montane African species of *Anotylus*, and reach their extreme expression in *A. leleupi* (Fagel) and *A. parasitus* (Bernhauer). In these two species, both formerly placed in *Oncoparia*, the elytra are vestigial, the central portion of the scutellum is much reduced and lacking in surface impressions and, as a result of great reduction in size of the meso- and meta-sternum, the meso-coxae are more or less contiguous.

Several morphological features may be regarded as typical of those *Anotylus* species which inhabit dung. Unusually stout tibiae bearing numerous blunt spines, presumably an adaptation for burrowing, are found in several groups. Setae which, for Oxytelinae, are of unusual structure occur in a number of the smaller dung-inhabiting *Anotylus*, e.g. *A. fairmairei* (Pandellé), *A. latiusculus* (Kraatz), etc. In these species the major setae on the dorsum of the head, pronotum and abdomen are short, somewhat flattened, and truncate. The few species of *Anotylus* with particularly large eyes and large eye facets, e.g. *A. ocellaris* (Fauvel), *A. testaceus* (Motschulsky), etc., are all inhabitants of dung or other particulate and ephemeral habitats. The same types of habitat are occupied by the much greater number of *Oxytelus* species with equally large eyes, e.g. *O. varipennis* (Kraatz), etc. (see Hammond, 1975a).

Sexual dimorphism is frequently marked in species of *Anotylus*. Males are generally characterized by a greater development of the fore-parts. In particular, the temples in this sex are frequently large, so that the eyes are less convex and appear to be less prominent than those of females. The antennae and maxillary palpi may also be slightly, occasionally markedly, longer and more robust in males. Species in which males exhibit pronounced secondary sexual modifications of the head, including a variety of horns, protuberances or other outgrowths, sometimes asymmetrical, are to be found in a number of species-groups. Such modifications are commonest and most marked in species native to the Neotropics or the Oriental-Australasian region. In some cases, considerable differences between the sexes in surface sculpture of the head and pronotum are associated with gross structural differences of these parts. The expression of male secondary sexual characteristics of the fore-parts is extremely variable in many *Anotylus* species. Infra-specific variation parallels that well-known in groups such as the Coprinae (Scarabaeidae).

'Major' and 'minor' males may be recognized – those of several species are illustrated by Steel (1948; 1954; 1955) – although a range of intermediates between the most major of males and female-resembling minors generally occurs. Male secondary sexual characteristics exhibited by the sternites of various abdominal segments (most commonly the 7th and/or 8th, occasionally the 5th or 6th) are of general occurrence in *Anotylus*. However, in many instances, much more commonly than in *Oxytelus*, such characteristics are inconspicuous (e.g. *crassicornis*-group discussed by Hammond (in press)). Relatively outstanding male abdominal features are found in a number of species-groups. Some of these have been illustrated by earlier authors, e.g. Cameron (1930), Fagel (1957; 1965), Lohse (1964), Palm (1961), Steel (1954), but those figured represent no more than a small part of the range of variation exhibited by *Anotylus* males.

The characters most useful for species recognition and diagnosis in *Anotylus* vary considerably according to the species-group, and no attempt will be made to discuss these fully here. Size, colour, vestiture, surface sculpture, detailed form and proportions of many different parts, may differ sufficiently to enable ready distinction of closely related species. For reasons already discussed by Hammond (1970) I have found the size of eyes and of eye facets particularly useful in diagnosis of species. However, unusually great infraspecific variation in eye size has been detected in a few *Anotylus* species. Inter-population differences in this respect appear to be exhibited by some species inhabiting tropical forest humus at high altitude (see discussion of *A. besucheti* Hammond and *A. distincticollis* (Cameron) provided by Hammond, 1975a). The value of male sexual characteristics for species discrimination is particularly variable in *Anotylus*. Differences between closely related species in male secondary sexual characteristics of the fore-parts may be marked and are frequently diagnostic. However, as noted above, males of many species are polymorphic in respect to development of the fore-parts. In such cases, investigation of the full range of infra-specific variation is essential if males are to be identified on this basis alone. Male abdominal structure varies little in a number of species-groups (e.g. *crassicornis*-group discussed by Hammond (in press)), and is frequently of relatively little diagnostic value. Even in some instances where conspicuous abdominal modifications are exhibited by males, interspecific differences may be small and comparative, e.g. species resembling *A. rugosus* (F.). Species-groups in which diagnostic male secondary sexual features are generally lacking may include a few, generally sympatric, species which exhibit pronounced species-specific modifications to the male abdomen. In a few groups, male abdominal modifications differing markedly between closely related species are of more or less general occurrence, e.g. species resembling *A. fairmairei* (Pandellé) and *A. pumilus* (Erichson). It is likely that many structures of this type are involved, as species-specific recognition devices, in the maintenance of reproductive isolation between certain sympatric species. The nature and extent of interspecific differences in male secondary sexual features are particularly varied in *Anotylus*. Further study of these features, therefore, may be instructive with regard to the significance of different speciation patterns with which these various structures are likely to be associated. It is already clear that presence or absence of outstand-

ing differences in male secondary sexual structures, between sister or closely related species, is correlated with particular characteristics of range, habitat and habits.

The primary sexual characteristics of *Anotylus* species have been largely ignored in previous systematic studies. Figures of the male genitalia of a few species have been provided by Coiffait & Saiz (1968), Fagel (1957; 1965), Hammond (1975a), Lohse (1964) and Steel (1954; 1955). My own studies to date suggest that the form of the median lobe (Text-figs 15-17), including internal structures, generally differs little between closely related species, and is of limited value in diagnosis of species-groups. The form of the lateral lobes, however, varies in a manner comparable, probably both in structural and functional terms, with male secondary sexual modifications of the abdominal sternites. In many groups differences between closely related species, including those which are sympatric, are slight, e.g. the *rufus*-group (Hammond, 1975a: figs 52-55), the *crassicornis*-group (Hammond, in press, figs 6-11, 14-23), etc., while in others they are marked. In at least one group of species, those resembling *A. fairmairei*, strikingly different structures are exhibited by the two lateral lobes of the same individual, rendering the genitalia asymmetrical. In several species-groups a few species only exhibit striking developments of the lateral lobes. For example, the lateral lobes of *A. inustus* (Gravenhorst), *A. plagiatus* (Rosenhauer), and many other members of the 'sculpturatus-group' are of simple form apically and virtually indistinguishable from each other. On the other hand, in two species of the same group, *A. sculpturatus* (Gravenhorst) and its undoubted sister species, *A. mutator* (Lohse), the apical portion of the lateral lobes is of substantially different structure from that of the others; differences between the two species are also marked.

A discussion of some of the features likely to be of value in constructing a phylogenetic classification of the *Anotylus* group is provided by Herman (1970: 415-417), and no attempt will be made to expand this greatly here. However, a few of the morphological features which may prove particularly significant in assessing relationships will be briefly considered. I have found a great variety of characters useful in establishing provisional phylogenetic hypotheses concerning the species presently contained in *Anotylus* and other genera of the *Anotylus* group. These include the form of the clypeus and supra-antennal prominences, presence or absence of a post-ocular furrow or ridge, condition of the occipital groove, variations in antennal structure (see below), form and proportions of maxillary palpal segments, form of the pronotum (including condition of the lateral borders, presence or absence of marginal and discal grooves and ridges, form of the elytra (including condition of the suture), form and vestiture of the tibiae, proportions of the tarsal segments and of the tarsus in relation to the tibia, relative breadths of the abdominal latero-sternites, chaetotaxy, particularly of the fore-parts (see below), structure of the 9th and 10th abdominal segments and both primary and secondary male sexual characteristics. A number of these characters, although clearly helpful in delimiting minor monophyletic groups, relate to structural features in which parallel developments are likely to be common within the *Anotylus* group. Much of the variation in form and vestiture of the tibiae and tarsi is probably of this type. For example, dorso-ventral flattening of the first tarsomere (found in *Rimba* as well as some

Anotylus species), although likely to have been derived more than once within the *Anotylus* group, is of diagnostic value for those groups in which it occurs. The partial classification of species now placed in *Anotylus* and *Oxytelus* provided by Fagel (1956, etc.), on the basis of 'types' of antennal segment, has been justly criticized by Herman (1970). However, my own studies (unpublished) of antennal variation throughout the Staphylinidae indicate that the antennae of Oxytelini are particularly rich in characters useful at a variety of levels. If due emphasis is placed on detection of the many probable parallel and convergent developments within the *Anotylus* group, antennal characteristics, including details of form, surface sculpture and vestiture of individual segments, as well as presence or absence of basal ridges, may be employed in definition of most monophyletic groups (Text-figs 19-24). A useful antennal character not noted by Fagel (1956) or Herman (1970) is the presence, in *Rimba* and certain groups of *Anotylus*, of a 'dorso-basal plaque' on the second segment, a development facilitating backwards folding of the antennae.

Although of largely similar form in most *Anotylus* (Text-figs 35-37), surface impressions on the scutellum provide information of diagnostic value for certain species-groups. An elongate impression of the type figured by Herman (1970: fig. 45) is characteristic of all members of an undoubtedly monophyletic group of species resembling *A. aliiceps* (Cameron) and *A. mirus* (Bernhauer). The elongate impression of slightly differing form, exhibited by *A. latiusculus* (Kraatz) and a number of similar species, may have been independently derived. Chaetotaxy has been previously ignored in systematic work on Oxytelini and most other Staphylinidae. However, the number and arrangement of setigerous pores on the foreparts has been found useful in diagnosis of *Anotylus* species-groups (e.g. *crassicornis*-group discussed by Hammond, in press). Further investigations are needed before the primitive arrangement of these pores in Oxytelini can be predicated with any confidence.

Certain variations in structure of the 9th and 10th abdominal segments may eventually prove to be of value in recognition of major lineages within the *Anotylus* group. The presence or absence of a V-shaped pattern of spinules on the 10th tergum, first noted by Herman (1970), appears to be useful in the diagnosis of major groups, although it is not yet clear how many times this apparently primitive feature has been lost in *Anotylus*. Other characteristics of the 10th tergum, the extent to which this tergum divides the 9th, and the position of glandular openings in the latter, also appear to be of potential classificatory significance.

Male secondary sexual structures provide much information of value in recognition of monophyletic groups. For example, males of the *rufus*-group (see Hammond, 1975a) may be recognized by the presence of characteristic protuberances on the vertex of the head, a feature no doubt uniquely derived in this group. Males of all species in the well-delimited *rugosus*-group exhibit striking yet similar modifications of the abdominal sternites. Male genitalia are also rich in characters useful in assessing relationships. Studies to date suggest that the form of the lateral lobes, which appear to conform to two principal types within the *Anotylus* group, will prove of particular value. Those of one type are more distinctly 'elbowed' basally

and, to a greater or lesser extent, embrace the sides and envelop the apex of the medial lobe (e.g. Text-fig. 15), while those of the second type lie flat on the ventral surface of the median lobe and do not envelop its apex (e.g. Steel, 1955: figs 5, 6). Either or both of these types may prove to incorporate conditions which have been uniquely derived within the *Anotylus* group.

NOMENCLATORIAL AND SYNONYMIC NOTES ON SPECIES

The notes that follow are intended to supplement the list of species included in *Anotylus* by Herman (1970: 417-421). It is felt unnecessary to repeat this list here or to provide a comprehensive bibliographical account of those species included, in *Anotylus* by Herman. In most instances no reference to the original descriptions of species is made by Herman (loc. cit.) but these references may be obtained in every case from the catalogues of Bernhauer & Schubert (1911), Scheerpeltz (1933) or the *Zoological Record* for the years following 1931.

The great majority of the 313 species included by Herman (loc. cit.) in *Anotylus* were so assigned on the basis of examination of primary type-material. In all but 10 cases specimens from the original type-series or apparently reliably identified specimens of the species in question were examined. I have also been able to examine typical material of almost all of these species and, without exception, agree with Herman (loc. cit.) regarding their inclusion in *Anotylus* as presently defined. However, further studies demonstrate the need for minor corrections to Herman's list of *Anotylus* species and indicate that a number of other species should be included.

Minor errors in the list of *Anotylus* species provided by Herman (1970).

'*A. curtusi* (Bernhauer)' (p. 418) is a misprint for *A. curtus* (Bernhauer).

'*A. hostilus* (Bernhauer)' (p. 418) is a misprint for *A. hostilis* (Bernhauer).

A. longicornis (Fauvel) was transferred to *Anotylus* from *Delopsis* and not from *Oxytelus* (see Cameron, 1930a).

'*A. okahandjanu* (Bernhauer)' (p. 419) is a misprint for *A. okahandjanus* (Bernhauer).

'*A. tibialis* (Brown)' (p. 421) is a misprint for *A. tibialis* (Brown).

Nomina nuda

My attempts to locate descriptions of two of the species included by Herman (1970) in his list of *Oxytelus* species (p. 410) have failed and I believe that both should be regarded as nomina nuda. This list of *Oxytelus* species is of relevance here as the great majority of the species so included where unsupported by examination of type-material or reliably identified specimens are to be transferred to *Anotylus* (see below).

Oxytelus occidentalis Fauvel is listed in the catalogue of Bernhauer & Schubert (1911: 117) as an Australian species. I have seen no other reference to this name apart from that of Herman (1970: 410). Bernhauer & Schubert (loc. cit.) refer to a description in *Annali Mus. civ. Stor. nat. Genova* 10 (1877): 199. Although

this page is included in a work on Australian Staphylinidae by Fauvel (1877) it contains no mention of *O. occidentalis*. I have also been unable to find any mention of this name elsewhere in the same work, in other works of Fauvel or in the Fauvel collection.

Oxytelus punctiger Scheerpeltz (1933 : 1102) was proposed as a replacement name for *O. punctatus* Broun (1880 : 90), not Leconte (1877). However, no trace of *Oxytelus punctatus* has been found in the work of Broun (1880), in other works by the same author or in the Broun collection (BMNH). *Gryophaena punctata* was described by Broun (1880 : 88) and some confusion with this species is possible although examination of the type (BMNH) demonstrates that, as expected, this species is a member of the subfamily Aleocharinae.

Additions to the list of *Anotylus* species provided by Herman (1970)

The following 56 species, most of them included by Herman (1970) in other genera, are here regarded as members of the genus *Anotylus*, although not included by Herman (loc. cit.) in that genus. These all stand, at least for the moment, as valid species of *Anotylus*; other names included in the present work for the first time in *Anotylus* are noted in the section below dealing with new synonymy. Where primary type-material has been examined this is indicated by the parenthetic use of 'examined'.

- A. athenensis* (Dvorak, 1954, **comb. n.** (from *Oxytelus*)
A. besucheti Hammond, 1975a [examined]
A. brincki (Scheerpeltz, 1974), **comb. n.** (from *Oxytelus*) [examined]
A. bruchi (Bernhauer, 1939), **comb. n.** (from *Oxytelus*)
A. cavicola (Bernhauer, 1926), **comb. n.** (from *Oxytelus*)
A. clavatus (Strand, 1946), **comb. n.** (from *Oxytelus*)
A. corcyranus (Coiffait, 1968), **comb. n.** (from *Oxytelus*)
A. crebratus (Schubert, 1906), **comb. n.** (from *Oxytelus*) [examined]
A. ebonus (Blackwelder, 1944), **comb. n.** (from *Oxytelus*) [examined]
A. exiguus (Erichson, 1840), **comb. n.** (from *Oxytelus*) [examined]
A. flavipennis (Kraatz, 1859), **comb. n.** (from *Oxytelus*) [examined]
A. forsteri (Scheerpeltz, 1960), **comb. n.** (from *Oxytelus*) [examined]
A. fortesculpturatus (Scheerpeltz, 1964), **comb. n.** (from *Oxytelus*)
A. foveicollis (Scheerpeltz, 1964), **comb. n.** (from *Oxytelus*)
A. gedyei (Bernhauer, 1936), **comb. n.** (from *Oxytelus*) [examined]
A. gibbulus (Eppelsheim, 1877), **comb. n.** (from *Oxytelus*) [examined]
A. hameedi (Abdullah & Qadri, 1970), **comb. n.** (from *Neoplatystethus*)
A. henryi (Fernando, 1960), (from *Deinopsis*, see Hammond, 1975b)
A. jarrigei **nom. n.**
 = *A. fageli* (Jarrige, 1970 : 60), **comb. n.** (from *Delopsis*), not *A. fageli* Herman (1970 : 418)
A. lateralis (Lea, 1906), **comb. n.** (from *Oxytelus*) [examined]
A. leleupi (Fagel, 1965), **comb. n.** (from *Oncoparia*) [examined]
A. lobatus (Fauvel, 1904), **comb. n.** (from *Oxytelus*) [examined]
A. loebli Hammond 1975a [examined]
A. magniceps (Wendeler, 1955), **comb. n.** (from *Oxytelus*) [examined]
A. mahmoodi (Abdullah & Qadri, 1970), **comb. n.** (from *Platystethus*)
A. marginatus (Weise, 1877), **comb. n.** (from *Oxytelus*) [examined]
A. meccii (Abdullah & Qadri, 1970), **comb. n.** (from *Neoplatystethus*)
A. micans (Kraatz, 1859) (from *Oxytelus*, see Hammond, 1975a) [examined]

- A. micros* (Scheerpeltz, 1974), **comb. n.** (from *Oxytelus*) [examined]
A. mixtus (Bernhauer, 1936), **comb. n.** (from *Oxytelus*)
A. mutator (Lohse, 1963), **comb. n.** (from *Oxytelus*)
A. myops (Fauvel, 1877), **comb. n.** (from *Oxytelus*)
A. nitescens (Bernhauer, 1942), **comb. n.** (from *Oxytelus*)
A. oblongifer (Lea, 1931), **comb. n.** (from *Oxytelus*) [examined]
A. occultus (Eichelbaum, 1913), **comb. n.** (from *Oxytelus*)
A. parasitus (Bernhauer, 1936), **comb. n.** (from *Oncoparia*) [examined]
A. pedator (Eichelbaum, 1913), **comb. n.** (from *Oxytelus*)
A. peruvianus (Bernhauer, 1941), **comb. n.** (from *Oxytelus*) [examined]
A. planicollis (Scheerpeltz, 1964), **comb. n.** (from *Oxytelus*)
A. plumbeus (Fauvel, 1878), **comb. n.** (from *Oxytelus*)
A. pluvius (Blackwelder, 1943), **comb. n.** (from *Oxytelus*)
A. quinquesulcatus (Bernhauer, 1908), **comb. n.** (from *Oxytelus*)
A. robusticornis (Luze, 1904), **comb. n.** (from *Oxytelus*)
A. sanctus (Scheerpeltz, 1962), **comb. n.** (from *Oxytelus*)
A. seydeli (Fagel, 1957), **comb. n.** (from *Anotylops*) [examined]
A. shafqati (Abdullah & Qadri, 1970), **comb. n.** (from *Neopyctocraerus*)
A. spinicornis Hammond (1975a) [examined] = *minutus* (Cameron, 1946) (from *Platystethus*),
not *Anotylys minutus* (Cameron, 1929)
A. styricola (Strand, E., 1917), **comb. n.** (from *Oxytelus*)
A. sutteri (Scheerpeltz, 1957), **comb. n.** (from *Oxytelus*) [examined]
A. tasneemae (Abdullah & Qadri, 1970), **comb. n.** (from *Platystethus*)
A. tenuesculpturatus (Scheerpeltz, 1964), **comb. n.** (from *Oxytelus*)
A. trisulcicollis (Lea, 1906), **comb. n.** (from *Oxytelus*) [examined]
A. tunariensis (Scheerpeltz, 1960), **comb. n.** (from *Oxytelus*) [examined]
A. ussuricus (Tichomirova, 1973), **comb. n.** (from *Oxytelus*)
A. v-elevatus (Lea, 1906), **comb. n.** (from *Oxytelus*) [examined]
A. zavadili (Roubal, 1941), **comb. n.** (from *Oxytelus*)

Although most of the species transferred above to *Anotylys* were listed under *Oxytelus* by Herman (1970) their inclusion here in the former genus does not represent any substantial departure from Herman's generic concepts. In the absence of firm evidence from the examination of type-material or elsewhere for their inclusion in *Anotylys* such species were correctly retained by Herman (loc. cit.) in *Oxytelus*. However, I have transferred to *Anotylys* three species, *Oxytelus ebonus* Blackwelder, *O. gedyei* Bernhauer and *Platystethus minutus* Cameron, which were retained in their original genera by Herman (loc. cit.) on the basis of his examination of types. As the typical material which I have examined of each of these species conforms to the diagnosis of *Anotylys* provided by Herman (loc. cit.) as well as to that given here their previous omission from that genus is likely to be due to oversight.

The types of several species retained by Herman (1970) in *Oxytelus* and which remain so placed have not been examined by either that author or myself. Of these, *O. aurantiacus* Fairmaire, *O. brasiliensis* Sahlberg, *O. kaltenbachi* Scheerpeltz, *O. mammillatus* Hochhuth, *O. methnerianus* Bernhauer, *O. murecarius* Bernhauer, *O. novaecaledoniae* Scheerpeltz and *O. tuberculifrons* Eichelbaum are retained in *Oxytelus* pending further investigation, although some are likely to be transferred to *Anotylys* in due course. Types of some of these (see under 'type-material' above) are known to be destroyed or are unavailable for examination. One species

of another genus, *Rimba birmana* (Scheerpeltz), is also probably to be transferred to *Anotylus*. In this case a new name may be necessitated due to preoccupation by *Anotylus birmanus* (Cameron). Although transferred above from *Oxytelus* to *Anotylus* one other species must be regarded as a *nomen dubium*. *Oxytelus styricola* was proposed by Strand (1917 : 82) as a replacement name for the preoccupied *Oxytelus humilis* of Gistel (1857 : 18). No Gistel type-material is known to exist and his description of this species renders its recognition uncertain. However, it is likely to be identical with one of the known European species of *Anotylus*, possibly *A. rugifrons* (Hochhuth).

Some of the species newly included in *Anotylus* in the list above, most of them described subsequent to Herman's studies, are not referred to in that author's work (1970). *Anotylus sanctus* (Scheerpeltz, 1962 : 565) appears to have been overlooked. *A. forsteri* (Scheerpeltz, 1960 : 72) and *A. tunariensis* (Scheerpeltz, 1960 : 74) are also omitted from mention by Herman (loc. cit.) and no reference to these species or others described in the same paper (Scheerpeltz, 1960) has been made in the *Zoological Record*. Four other species described in *Oxytelus*, *A. corcyranus* (Coiffait, 1968 : 95), *A. ussuricus* (Tichomirova, 1973 : 158), *A. brincki* (Scheerpeltz, 1974 : 67), *A. micros* (Scheerpeltz, 1974 : 70), two described in *Anotylus*, *A. besuchteti* Hammond (1975a), *A. loebli* Hammond (1975a), one described in *Deinopsis*, *A. henryi* (Fernando, 1960 : 7) and one described in *Delopsis*, *A. fageli* (Jarrige, 1970 : 60) are also additional to those included in the Oxytelinae by Herman (loc. cit.). As Jarrige's description of *Delopsis fageli* clearly demonstrates to me its distinctness from other previously described species of *Anotylus*, in which genus the name is preoccupied, a replacement name has been proposed above.

Although the transfer of *Oxytelus micans* Kraatz to *Anotylus* is noted above it should be made clear that the *Oxytelus micans* of all authors subsequent to Kraatz (1859) is a true *Oxytelus*. This species, widely distributed in the Old World tropics, is now to be known as *Oxytelus puncticeps* Kraatz (see Hammond, 1975a). It may also be noted that the species described by Scheerpeltz (1974 : 72) as *Oxytelus* (*Anotylus*) *traegardhi* is a true *Oxytelus* (see below under 'new synonymy').

Other species newly transferred to *Anotylus* fall into the synonymy of species already included in the genus and are referred to in the following section.

New synonymy

As the present work is largely introductory and a prelude to further taxonomic studies of the genus *Anotylus* I have not felt it appropriate to note all of the new synonymies which appear probably justified on the basis of studies to date. In several cases, e.g. *A. exasperatus* (Kraatz) (see Hammond, 1975a), allopatric populations which differ morphologically but which may be conspecific are represented by different names which currently enjoy specific status. As further studies may demonstrate an advantage in retaining such names to represent subspecies (or even for different species) no discussion of them is included here.

Two new synonymies are noted below in order to avert any unnecessary introduction of replacement names for junior homonyms. The remaining new synonymies

relate to species from faunas which are already well known or to species of the cosmopolitan and adventive type.

Some of the synonymies listed as new below have already been proposed or suggested by earlier authors. Cameron (1934) noted new synonymies involving species described by Motschulsky. Fauvel (1905) placed his own *Oxytelus celebensis* in the synonymy of '*Oxytelus thoracicus* Motschulsky' and recent European authors such as Lohse (1964) have regarded *Oxytelus ixellensis* Dvorak, *O. christiana* Bernhauer and *O. minarzi* Bernhauer as junior synonyms, 'aberrations' or 'varieties' of other species. In each of these cases the synonymies have been overlooked by cataloguers, including Herman (1970), and by the *Zoological Record*. *Aploderus testaceus* Cameron is listed, as such, by Scheerpeltz (1933), but is not mentioned under *Aploderus* or any other genus by Herman (1970). It falls into the synonymy of *Oxytelus testaceus* Motschulsky (now in *Anotylus*).

The following depositories are indicated in the list of new synonymy by the abbreviations which precede them.

MNHU, Berlin	Museum für Naturkunde, Humboldt-Universität, Berlin.
IRSNB, Brussels	Institut Royal des Sciences Naturelles de Belgique, Brussels.
BMNH	British Museum (Natural History), London.
CSIRO, Canberra	C.S.I.R.O. Division of Entomology, Canberra.
DEI, Eberswalde	Deutsches Entomologisches Institut, Eberswalde, East Germany [Now Institut für Pflanzenschutzforschung Kleinmachnow, Abteilung Taxonomie der Insekten.]
ZM, Moscow	Zoological Museum, University of Moscow, Moscow.
MRAC, Tervuren	Musée Royal de l'Afrique Centrale, Tervuren, Belgium.
NM, Vienna	Naturhistorisches Museum, Vienna.

Anotylus aliiceps (Cameron, 1950c : 181 (*Oxytelus*)). Holotype ♂, KENYA (BMNH) [examined].

Oxytelus (*Anotylus*) *transversefoveolatus* Scheerpeltz, 1974 : 69. Holotype ♀ (not ♂ as stated by Scheerpeltz, 1974 : 70), SOUTH AFRICA (University of Lund) [examined]. **Syn. n.**

Anotylus bernhaueri (Ganglbauer, 1898 : 400 (*Oxytelus*)). LECTOTYPE ♂, AUSTRIA (NM, Vienna), here designated [examined].

Oxytelus (*Anotylus*) *Minarzi* Bernhauer, 1936c : 185. Holotype ♂, AUSTRIA (Field Museum of Natural History, Chicago). **Syn. n.** [Already in *Anotylus*.]

Oxytelus (*Anotylus*) *Christiana* Bernhauer, 1939 : 70. Holotype ♂, AUSTRIA (Field Museum of Natural History, Chicago). **Syn. n.** [Already in *Anotylus*.]

Anotylus brunneipennis (MacLeay, 1873 : 150 (*Oxytelus*)). Syntypes, AUSTRALIA (CSIRO, Canberra) [2 ♂ syntypes examined].

Oxytelus (*Anotylus*) *crookesi* Cameron, 1950d : 23. Syntypes, NEW ZEALAND (1 ♂, 1 ♀ in D.S.I.R., Division of Entomology, Auckland, 1 ♀ in BMNH) [examined]. **Syn. n.** [Already in *Anotylus*.]

Anotylus caffer (Erichson, 1840 : 790 (*Oxytelus*)). Syntypes, SOUTH AFRICA (MNHU, Berlin) [2 ♂ syntypes examined].

Oxytelus picipennis Boheman, 1848 : 295. Syntypes, SOUTH AFRICA (Naturhistoriska Riksmuseet, Stockholm) [2 ♀ syntypes examined] (primary homonym of *Oxytelus picipennis* Stephens, 1834 : 316). **Syn. n.**

Oxytelus bohemani Bernhauer & Schubert, 1911 : 110 (replacement name for *Oxytelus picipennis* Boheman). **Syn. n.**

- Oxytelus (Anotylus) Christophersenii* Brinck, 1948 : 28. Syntypes, TRISTAN DA CUNHA (Zoological Museum, Oslo & University of Lund) [5 topotypical specimens examined]. **Syn. n.** [Already in *Anotylus*.]
- Oxytelus (Anotylus) rudebecki* Scheerpeltz, 1974 : 66. Holotype ♀, SOUTH AFRICA (University of Lund) [examined]. **Syn. n.**
- Anotylus cephalotes* (Eppelsheim, 1895 : 66 (*Oxytelus*)). Syntypes, INDIA (MNHU, Berlin & NM, Vienna) [2 ♂, 3 ♀ syntypes examined].
- Oxytelus tibialis* Schubert, 1908 : 624. Syntypes, INDIA (MNHU, Berlin) [1 ♂ syntype examined], (secondary homonym of *Oxytelus tibialis* (Broun, 1880 : 120 (*Omalium*)); synonym of *Anotylus semirufus* (Fauvel)). **Syn. n.**
- Oxytelus Schuberti* Scheerpeltz, 1933 : 1103 (replacement name for *Oxytelus tibialis* Schubert). **Syn. n.**
- Anotylus complanatus* (Erichson, 1839 : 595 (*Oxytelus*)). Syntypes, GERMANY (NMHU, Berlin) [5 ♂, 4 ♀ syntypes examined].
- Oxytelus (Anotylus) ixellensis* Dvorak, 1954 : 41. Holotype ♂, BELGIUM (Dvorak collection) [topotypical specimens examined]. **Syn. n.**
- Anotylus chilensis* Coiffait & Saiz, 1968 : 420. Holotype ♂, CHILE (Catholic University of Valparaiso) [topotypical specimens from Saiz collection examined]. **Syn. n.**
- Anotylus fragilis* (Sharp, 1887 : 691 (*Oxytelus*)). Syntypes, GUATEMALA & PANAMA (BMNH) [13 syntypes (unsexed) examined].
- Oxytelus minimus* Erichson, 1840 : 789. Syntypes, COLOMBIA (MNHU, Berlin) [2 ♂, 3 ♀ syntypes examined] (primary homonym of *Oxytelus minimus* Runde, 1835 : 20; now in *Carpelimus*). **Syn. n.**
- Anotylus impressifrons* (MacLeay, 1873 : 150 (*Oxytelus*)). Syntypes, AUSTRALIA (CSIRO, Canberra) [1 ♂, 1 ♀ syntypes examined].
- Oxytelus flavior* Blackburn, 1902 : 24. Syntypes, AUSTRALIA (BMNH) [1 ♂ syntype examined]. **Syn. n.** [Already in *Anotylus*.]
- Anotylus inustus* (Gravenhorst, 1806 : 188 (*Oxytelus*)). Holotype (? sex), ?GERMANY (? lost (Knoch collection)).
- Oxytelus excavatus* Motschulsky, 1857 : 503. Syntypes, ALGERIA (ZM, Moscow) [2 ♂ syntypes examined] (not a synonym of *Platystethus oxytelinus* Fauvel). **Syn. n.**
- Anotylus lewisius* (Sharp, 1874 : 95 (*Oxytelus*)). Holotype ♀, JAPAN (BMNH) [examined].
- Oxytelus (Anotylus) similis* Cameron, 1930b : 184. Holotype ♂, JAPAN (BMNH) [examined]. **Syn. n.** [Already in *Anotylus*.]
- Anotylus lippensi* (Bernhauer, 1943 : 277 (*Oxytelus*)). Syntypes, ZAIRE (IRSNB, Brussels & (?) FMNH, Chicago) [1 ♂ syntype examined].
- Oxytelus* (s. str.) *armatus* Cameron, 1950a : 8. Holotype ♂, ZAIRE (MRAC, Tervuren) [examined] (primary homonym of *Oxytelus armatus* Say, 1823 : 155; now in *Bledius*). **Syn. n.** [Already in *Anotylus*.]
- Anotylus marginatus* (Weise, 1877 : 96 (*Oxytelus*)). Syntypes, JAPAN (DEI, Eberswalde) [1 ♀ syntype examined].
- Oxytelus (Anotylus) sharpianus* Cameron, 1930b : 184. Holotype ♀, JAPAN (BMNH) [examined]. **Syn. n.** [Already in *Anotylus*.]
- Anotylus nitidulus* (Gravenhorst, 1802 : 107 (*Oxytelus*)). Syntypes, GERMANY (MNHU, Berlin).
- Oxytelus borealis* Motschulsky, 1860 : 119. Syntypes, U.S.S.R. (ZM, Moscow) [11 syntypes examined]. **Syn. n.**
- Anotylus pygmaeus* (Kraatz, 1859 : 176 (*Oxytelus*)). Syntypes, SRI LANKA (DEI, Eberswalde) [2 ♂, 3 ♀ syntypes examined].
- Oxytelus Sauteri* Bernhauer, 1907 : 375. Syntypes, JAPAN (Field Museum of Natural History, Chicago; NM, Vienna) [1 ♂ syntype examined]. **Syn. n.** [Already in *Anotylus*.]

- Anotylus semirufus* (Fauvel, 1878 : 493 (*Oxytelus*)). Syntypes, AUSTRALIA (IRSNB, Brussels) [4 syntypes examined].
Omalium tibialis Broun, 1880 : 120. Holotype ♀, NEW ZEALAND (BMNH) [examined].
Syn. n. [Already in *Anotylus*.]
- Anotylus subsculpturatus* (Cameron, 1928 : 101 (*Oxytelus*)). Syntypes, SUMATRA (BMNH) [2 ♂, 1 ♀ syntypes examined].
Oxytelus (Anotylus) masuriensis Cameron, 1930 : 244. Syntypes, INDIA (BMNH) [2 ♂, 2 ♀ syntypes examined]. **Syn. n.** [Already in *Anotylus*.]
Oxytelus (Anotylus) morbosus Cameron, 1942 : 106. Holotype ♂, INDIA (BMNH) [examined].
Syn. n.
- Anotylus testaceus* (Motschulsky, 1857 : 506 (*Platystethus*)). Syntypes, 'INDIA ORIENTALI' (ZM, Moscow) [2 ♀ syntypes examined].
[*Oxytelus thoracicus* Motschulsky sensu auct. Misidentification: this species is now in *Coenonica*.]
Oxytelus celebensis Fauvel, 1886 : 145. Syntypes, CELEBES (IRSNB, Brussels) [2 ♂, 5 ♀ syntypes examined]. **Syn. n.**
Aploderus testaceus Cameron, 1918 : 65. Syntypes, SINGAPORE (BMNH) [1 ♂ syntype examined]. **Syn. n.**
Oxytelus (Caccoporus) aequicollis Bernhauer, 1936a : 81. Syntypes, PHILIPPINES (Field Museum of Natural History, Chicago) (1 ♂ syntype examined). **Syn. n.**
- Anotylus vinsoni* (Cameron, 1936 : 201 (*Oxytelus*)). Syntypes, MAURITIUS (BMNH) [1 ♂ syntype examined].
[*Oxytelus sparsus* Fauvel sensu auct. Misidentification.]
Oxytelus chapini Blackwelder, 1943 : 101. Holotype ♂, JAMAICA (United States National Museum, Washington) [4 paratypes examined]. **Syn. n.** [Already in *Anotylus*.]
- Anotylus wattsensis* (Blackburn, 1902 : 23 (*Oxytelus*)). Syntypes, AUSTRALIA (BMNH) [1 ♂, 1 ♀ syntypes examined].
Oxytelus curtus Bernhauer, 1904 : 219. Syntypes, AUSTRALIA (Field Museum of Natural History Chicago; BMNH) [1 ♀ syntype examined]. **Syn. n.** [Already in *Anotylus*.]
- Oxytelus fulgidus* Fauvel, 1905 : 123. Syntypes, KENYA & 'ZAMBÈSE' (IRSNB, Brussels) [4 (unsexed) syntypes examined].
Oxytelus (Anotylus) traegardhi Scheerpeltz, 1974 : 72. Holotype ♂, SOUTH AFRICA (University of Lund) [examined]. **Syn. n.**
- Coenonica thoracica* (Motschulsky, 1857 : 504 (*Oxytelus*)). Syntypes, 'INDIA ORIENTALI' (ZM, Moscow) [1 ♂ syntype examined]. **Comb. n.**
Coenonica stricticollis Cameron, 1921 : 241. Syntypes, SINGAPORE (BMNH) [4 (unsexed) syntypes examined]. **Syn. n.**

In addition to the new synonymy listed above, two species listed under *Oxytelus* and seven species listed under *Anotylus* by Herman (1970) have already been relegated to the synonymy of other species of *Anotylus* (Hammond, 1975a), and three further synonymies are noted in a discussion of the *crassicornis*-group provided by Hammond (in press).

Two previously unrecognized instances of primary homonymy (*Oxytelus armatus* and *Oxytelus minimus*) are noted in the list of new synonymy above. I have come across two further cases in the genus *Anotylus* where the junior primary homonym represents a species currently regarded as valid. In both of these cases, *A. longicornis* (Fauvel) and *A. pygmaeus* (Kraatz), the species were described in *Oxytelus*. Both names are preoccupied by others which have had no currency as valid names for

more than one hundred years. As no useful purpose would appear to be served by replacing the established junior names, they are retained here.

IMMATURE STAGES

The work of Kasule (1966) enables the satisfactory recognition of larvae belonging to the subfamily Oxytelinae. A key to the genera known, as larvae, to that author is provided by Kasule (1968), in which *Oxytelus* (s. l., incorporating *Anotylus*) is included. The very few larvae of Oxytelini which have been characterized, belonging to the genera *Anotylus*, *Oxytelopsis*, *Oxytelus* and *Platystethus*, differ very little amongst themselves in structure. They may be distinguished from larvae of generally similar form of other genera of Oxytelinae which have been described (*Bledius*, *Carpelimus*, *Ochtheophilus* Mulsant & Rey, *Thinobius* Kiesenwetter) by the possession of no more than one ocellus on each side of the head. Larvae of *Anisopsidius*, *Anisopsis*, *Apocellus*, *Hoplitodes*, *Paroxytelopsis* and *Rimba*, all of which remain undescribed, are likely to resemble those of the *Anotylus-Oxytelus* group. Likely characteristics of the so far unknown larvae of *Aploderus* and *Paraploderus* Herman are less easy to predict although either or both genera may prove to have much in common with the *Anotylus-Oxytelus* group. A larva, named as *Aploderus caelatus* (Gravenhorst) by association with adults taken in dung, which I have examined (BMNH) is scarcely distinguishable from those of *Anotylus*, but may well prove to be misidentified and belong to a species of the latter genus.

I have encountered published descriptions of larvae of only five species now placed in *Anotylus* and none of eggs and pupae. Larvae of *A. inustus* (Gravenhorst), *A. rugosus* (F.), *A. sculpturatus* (Gravenhorst) and *A. tetracarinatus* (Block) have each been described and figured (as species of *Oxytelus*) by several authors. All, except *A. tetracarinatus*, are included by Paulian (1941). A further species, *A. hybridus* (Eppelsheim), is figured by Pototskaya (1967). The most satisfactory description is probably that of *A. tetracarinatus* given by Verhoeff (1919), who includes notes on the internal organization and life-history of larvae of that species. The larva described by Paulian (1938) as that of *Oxytelus abnormalis* Cameron (now in *Anotylus*) was later recognized by the same author (Paulian, 1941) to be that of a member of the subfamily Aleocharinae.

I have collected and bred larvae of Oxytelini, including *Anotylus*, *Oxytelus* and *Platystethus*, from various parts of the world. Study of these is incomplete, but it is already clear that larvae of these genera are extremely similar. As *Anotylus*, in the sense of the present paper, has only recently been regarded (Herman, 1970) as a genus distinct from *Oxytelus*, it is not surprising that no generic diagnosis relating to larvae is yet available. All *Anotylus* larvae which I have examined share many features with both *Oxytelus* and *Platystethus*. The majority would run to *Oxytelus* in existing keys while some might be referred to *Platystethus*. As many diagnostic characters relating to the proportions of parts are likely to vary considerably within each genus further study is necessary to enable satisfactory generic definitions and a workable key to the larvae of this group of genera.

However, of the few larvae which I have examined those of *Anotylus* have a longer prementum and maxillary palpi in which the penultimate segment is shorter in relation to the apical segment than is the case in *Platystethus*. Larvae of *Oxytelus* (s. str.) examined are more highly coloured, have a broader head and larger and more posteriorly situated ocelli than in *Anotylus*. A further feature in which larvae of *Oxytelus* and *Anotylus* examined differ is more likely to prove to be genuinely diagnostic. Spiracles of *Oxytelus* larvae examined are situated well within the pigmented tergites of the abdominal segments. Those of *Anotylus* are found at the lateral borders of the tergites or within the membrane between the tergites and sternites. This difference may be associated with the different positioning of spiracles in adults of the two genera. It should be noted that the size of larval ocelli is particularly likely to vary within the genus *Anotylus*, in which some adults are virtually eyeless and some species are largely subterranean. In some cases, as noted for the *Oxytelopsis* larva described by Paulian (1941), ocelli may be vestigial or even absent.

What little I have observed of the life-cycle of *Anotylus* species and the duration of larval development largely resembles that documented for *A. tetracarinatus* by Verhoeff (1919) and for *Platystethus arenarius* (Fourcroy) by Hinton (1944). The observations of Hafez (1939) on *Anotylus latiusculus* (Kraatz) in Egypt suggest that development for some species, at least in the warmer parts of the world, may be much speedier. Larvae of this species, which were present in dung on the 4th day after its deposition, pupated within 2 to 3 days and adults emerged some 4 days later. Although Hafez (1939) notes that '*Oxytelus*' larvae which he studied 'probably feed on mites or eggs of other insects' and that those of *A. latiusculus* are 'probably predaceous', all larvae of *Anotylus* which I have bred appeared to feed on the decaying vegetable matter or dung in which they were placed.

BIOLOGY

Little documented evidence regarding the feeding habits of species of *Anotylus* is available, but my own observations suggest that, like most (or all) other Oxytelini, members of this genus are not predators. I have been able to maintain populations of adults and larvae of a number of species from Europe and the Old World tropics through several generations in decomposing vegetable matter or dung which contained no other insects or other invertebrates visible to the naked eye. The belief that members of the subfamily Oxytelinae usually feed on vegetable matter finds expression, generally without documentation, in a number of works on Staphylinidae. The general account of feeding habits in Staphylinidae provided by Voris (1934) demonstrates that most members of the family are likely to be predators but, apart from a record of *Apocellus sphaericollis* Say damaging violets, no specific observations on Oxytelinae are included. Some species of *Bledius* and *Thinobius* are known to feed on algae or other vegetable matter and this habit is likely to be general in those Oxytelinae which burrow in waterside mud or sand. Species of *Anotylus* and allied genera such as *Oxytelus* are generally not ripicolous although this habit is found, apparently as a quite independent development from that of other Oxy-

telinae in some *Platystethus*. However, the variety of biotopes in which species of *Anotylus* are known to occur provides no conclusive evidence regarding their feeding habits.

Several recent accounts of the coleopterous inhabitants of dung and certain references to individual species of *Anotylus* assert that members of the genus are predatory on Diptera or other arthropods. Horion (1963) notes, without indicating a source, that *Anotylus insecatus* (Gravenhorst) has been recorded as a predator of fly maggots in the bulbs of garden plants. *A. insecatus* is known to be largely subterranean and has been found in numbers in decaying seed potatoes. Evidence for its predatory behaviour in such situations may rest on no more than association of adult *Anotylus* with dipterous larvae. It is not unusual for slender evidence of this type to be used in determining the predatory status of Staphylinidae and other Coleoptera, which further studies show to be saprophagous, mycetophagous or general scavengers. A member of a related genus, *Platystethus americanus* Erichson, is stated by Mohr (1943) to be a predator on the eggs of Diptera in cow dung. Legner & Olton (1970) include the same species in a list of those 'known to be predaceous on muscoid eggs and young larvae' and also include *Anotylus niger* (Leconte) in a list of 'potentially predatory species'. However, evidence in support of these views is not to be found in either of these papers and Wingo *et al.* (1974) demonstrate that *Platystethus americanus* arrives too late at cow manure in Missouri to predate the eggs or larvae of at least some species of Diptera. Lawrence (1954) also notes that most staphylinid larvae are to be found in dung after dipterous larvae have left. Hafez (1939) notes that Staphylinidae arrive fairly late in the succession at dung and, although regarding *Anotylus* larvae as probably predaceous, considers that adults of *A. latiusculus* 'probably feed on dung'.

My own view, based on collection of many thousands of specimens of *Anotylus* and rearing of several species, is that the feeding habits of at least those species which inhabit dung and decaying vegetable matter are likely to resemble those found by Hinton (1944) in *Platystethus arenarius* (Fourcroy). Hinton observed that both larvae and adults of *P. arenarius* would feed exclusively on cow dung, although they were facultative predators, and also noted that larvae of *Anotylus sculpturatus* fed on dung. Further detailed observations are clearly needed before confident generalizations concerning the food of *Anotylus* species and other Oxytelini can be made. The question is of some significance as Oxytelini are frequently very numerous in dung and other accumulations of organic debris. If at least some of them are predators they may play a large part in the control of fly populations. If, as I suspect, they are largely saprophagous or scavengers, they may play a considerable role in the break-down of organic debris, including herbivorous mammal dung in pastures. I know of no species of *Anotylus* or other genera of Oxytelinae which is particularly associated with decaying *animal* matter but records of a few species for carrion may indicate that products of animal putrefaction are also suitable as food.

Although no habitat data or biological information of any kind is presently available for the great majority of species, the range of habitats occupied by species of *Anotylus* is clearly broad. Situations in which European species of the genus

have been collected are discussed in many works, notably that of Horion (1963) who comments (under *Oxytelus*) on the life histories and usual habitats of 21 central European species. Such accounts, my own collections made in various parts of the world and label data associated with other material examined enable certain generalizations. Many species inhabit decaying organic matter of various kinds, a number of these principally or exclusively in dung. However, a large number, possibly the majority of species, are inhabitants of humus and leaf litter, primarily in tropical forests. The species of tropical rain forest are generally associated either with humus or rapidly decaying material such as fallen fruit, but not both types of habitat. In the more arid regions of the tropics few species are to be found except in dung. In temperate regions some species may be classified as inhabitants of litter and others are found in dung or decaying plant material of the compost type, while many appear to be catholic in occupation of a variety of habitats where organic debris occurs. The range of habitats favoured by most species of *Anotylus* may be seen as a spectrum in terms of relative permanence and the rate at which putrefaction of the substrate proceeds. The expression of synanthropic tendencies correlates well with this spectrum and, as illustrated below, it is largely those species typical of dung or rapidly decaying accumulations of organic debris which have, frequently with the aid of man, spread to occupy very broad geographical ranges.

A few species of *Anotylus* are known to favour habitats of more restricted occurrence. Several species are to be found occasionally in close proximity to salt water, but only one, *A. perrisi* (Fauvel), a north-west European species, is known to be more or less confined to the marine littoral. Adults and larvae of this species occur most commonly in accumulations of decaying seaweed and other organic material on the seashore. Several species have been collected from the nests of small mammals, two of which – *A. saulcyi* (Pandellé) and *A. bernhaueri* (Ganglbauer) – are known to be more or less confined to such situations. *A. saulcyi* has most frequently been found in the nests of moles but also in those of various mice, rats, hamsters, susliks, rabbits and badgers (Horion, 1963). *A. bernhaueri* is well-known as an inhabitant of burrows of the European suslik and has also been found in moles' nests. In North America *A. neotomae* (Hatch) has been taken in nests of the wood-rat (*Neotoma*), and in Argentina *A. murecarius* (Bernhauer) has been found in nests of *Ctenomys talanum* Thomson. The morphology of an undescribed African species of *Anotylus*, of which I have examined a series taken from the nests of mole-rats, suggests that it may be specially adapted to such situations. The almost eyeless *A. parasitus* (Bernhauer) has been found in association with a rodent's nest in Kenya but, as noted by Fagel (1965), this and the related species *A. leleupi* (Fagel) are likely to be edaphic rather than truly nidicolous. Several species of *Anotylus* are inhabitants of deep humus and may be effectively subterranean, but no evidence is available to suggest that any are truly cavernicolous. The few records of *Anotylus* species from caves all appear to relate to stray individuals. True myrmecophily in *Anotylus* also remains to be demonstrated. *A. placusimus* (Leconte) was described from ants' nests near Washington, U.S.A., and *A. myrmecophilus* (Cameron) from a number of specimens taken from a nest

of *Pheidologeton diversus* (Jerdon) in a decayed *Ficus* in southern India. However, like certain European species of *Anotylus* which have, on occasion, been found with ants, the association of these species with ants' nests may be only a casual one. A number of African species of *Oxytelus* and allied genera are commensals of doryline ants while others are termitophilous, but there is no evidence to suggest that species of *Anotylus* found in Africa have similar habits. On the other hand, in South and Central America, species of the closely related genus *Apocellus* (but none of *Oxytelus* or allied genera) appear to be frequently associated with ants.

I have examined a series of an undescribed Australian species of *Anotylus* which exhibits apparently kleptoparasitic behaviour. Although otherwise unknown to me, this species has been taken in numbers from the brood-balls of Scarabaeid beetles of the genus *Cephalodesmus*; individuals have also been observed on several occasions above ground mounted on the backs of and carried by *Cephalodesmus* (G. Monteith, personal communication).

Some species of *Anotylus* are able to achieve a considerable abundance in suitable habitats. For example, Hafez (1939) recorded an average of 808 individuals of *Anotylus latiusculus* (Kraatz) per pound of dung examined in Egypt. Bacchus & Hammond (1972) collected 941 individuals of *A. tetracarinatus* (Block) from 9 lbs 12 oz of donkey dung in England. My own experiences in collecting suggest that, in suitable concentrations of decaying organic material, such population densities are frequently exceeded. The dispersal behaviour of many species, especially those typical of temporary habitats, is such that their general abundance is frequently reflected in the numbers captured in traps for flying insects. As published results relating to trap catches rarely include mention of specifically identified Staphylinidae little quantitative data is available to illustrate this point. However, in samples collected by Freeman (1945) and by Lewis & Taylor (1965) Staphylinidae were more abundant than other families of Coleoptera. '*Oxytelus*' (mostly *Anotylus* in Britain) was one of the three best represented genera of Staphylinidae in Freeman's catches in southern England, while two species of *Anotylus* were among the most abundant of Staphylinidae in Lewis & Taylor's samples from Rothamsted. Omer-Cooper & Tottenham (1934) obtained some 7000 beetles of 81 species by sweeping the air with a hand-net for six hours, at about sunset on July evenings at Wicken Fen, England. *Anotylus nitidulus* (Gravenhorst) was represented in this collection by 4080 individuals, or some 59% of the catch, and *A. tetracarinatus* (Block) by 1920 individuals, 28% of the catch, which also included *A. complanatus* (Erichson), *A. rugosus* (F.) and *A. sculpturatus* (Gravenhorst). While using a net to catch flying insects from a bicycle B. S. Williams (1930) found *A. tetracarinatus* to be the most abundant beetle species captured. It may be noted that this species has been regarded, perhaps with some justification, as the most 'common' of European beetles. In northern Europe, although other small Staphylinidae and various Thysanoptera are also commonly involved, the familiar 'fly-in-the-eye' frequently turns out to be *A. tetracarinatus*.

As may be expected, it is the species typical of temporary habitats which are most frequently taken in flight. Indeed, a number of the species inhabiting relatively stable biotopes, such as forest humus, are wingless or brachypterous.

Although little data is available concerning the periodicity of flight in *Anotylus*, it is clear from anecdotal observations that most species exhibit considerable diurnal and crepuscular flight activity. It is likely that light intensity plays a part in determining the timing of flights in some species; such factors as emergence rhythms are probably of little significance. The role of temperature and humidity thresholds may be considerable and these are likely in many instances to effectively determine the duration of and peaks in flight activity. Variation of flight periodicity between species appears to correlate well with differences in habitat. Lewis & Taylor (1965) found that flight activity of *Anotylus complanatus* (Erichson) at Rothamsted in July 1962 was at a peak between 2 and 3 p.m., while that of *A. tetracarinatus* (Block) was at a peak between 4 and 5 p.m. Although some *Anotylus*, particularly the mat black species inhabiting dung, may exhibit largely diurnal flight activity, many species are abundant at or about dusk and some fly throughout the night. In the tropics night flight is likely to be a regular activity of some species, while in temperate areas nocturnal flight activity generally demands appropriately warm and muggy conditions. Although light-traps, involving as they do an attractant, are unlikely to provide reliable data concerning flight periodicity, the results of such trapping enable some comparisons between species to be made. Unlike many other genera of Oxytelinae, such as *Oxytelus*, *Bledius*, *Carpelimus*, *Thinobius*, etc., relatively few species of *Anotylus* are to be taken at light-traps. For example, in Africa as many as twenty or thirty species of *Oxytelus* may be represented in a single light-trap catch, while *Anotylus* species, even though several may occur in the immediate vicinity, are absent. I have seen no specimens of the generally abundant tropical dung-inhabiting species, *A. latiusculus*, taken at light, although I have frequently operated light-traps within a few feet of habitats containing dense populations of the species. However, diurnal flight of this species has been observed on many occasions and I have examined specimens taken in an aeroplane tow-net during day-time flights over East Africa. I have seen specimens of some twenty species of *Anotylus* taken at light, of which only nine (marked with an asterisk in the following list) have been collected frequently or abundantly in this way: *A. atriceps* (Fauvel), *A. bubalus* (Fauvel), *A. dilutipennis* (Fauvel)*, *A. exasperatus* (Kraatz), *A. glareosus* (Wollaston)*, *A. insignitus* (Gravenhorst)*, *A. loebli* Hammond, *A. nitidifrons* (Wollaston)*, *A. ocellaris* (Fauvel), *A. pygmaeus* (Kraatz), *A. rubidus* (Cameron), *A. rufus* (Kraatz)*, *A. rugosus* (F.), *A. sculpturatus* (Gravenhorst), *A. seydeli* (Fagel), *A. sparsus* (Fauvel)*, *A. stanleyi* (Cameron)*, *A. testaceus* (Motschulsky)*, *A. tetracarinatus* (Block), *A. vinsoni* (Cameron)*. The species known to fly to light are generally those of the most ephemeral habitats but include few which are more or less *specific* to dung. Species which have shown themselves to be successful colonists (see below), many of them relatively pale in colour, are particularly well represented in light-trap catches.

As most *Anotylus* species probably breed in as well as feed on decaying organic material, their flight activity includes both migratory and feeding components. There is no evidence to suggest any directly sexual content in these flights and they may conveniently be regarded as dispersal activities. For the species of temporary and highly fragmented habitats dispersal abilities are clearly of great importance.

The extremely rapid dessication of dung in Egypt, described by Hafez (1939), illustrates the speed with which some habitats exploited by *Anotylus* species become unsuitable for continued occupation.

ZOOGEOGRAPHY

As available distributional data for the majority of described species are few, and understanding of relationships between species poor, a full discussion of the zoogeography of *Anotylus* is not yet appropriate. Large numbers of species already represented in collections remain to be described, and many more, no doubt, still to be discovered. However, it is already clear that distributional characteristics exhibited by the genus, its component species-groups and species, are likely to provide considerable phylogenetic evidence, particularly with regard to the relative ages of sub-groups.

Anotylus is well represented in all major faunistic regions, with the exception of New Zealand. Apart from Arctic tundra, extensive deserts, oceanic islands and New Zealand, native species of *Anotylus* probably occur in every part of the world from about 65° N to about 40° S. The species composition of the faunas of certain areas, for example the western Palaearctic, may be regarded as fairly well established, but many species evidently await discovery in most parts of the tropics. The richest areas in species of *Anotylus* are undoubtedly the Neotropical and Oriental-Australasian regions (see Table 1). However, it is in the great centres

TABLE 1

Representation of *Anotylus* in various faunistic regions

Faunistic Region	Described species of <i>Anotylus</i>	Probable total number of species of <i>Anotylus</i>
Oriental-Australasian	178	270 to 380
Ethiopian-Lemurian	57	130 to 180
Palaearctic	55	64 to 80
Nearctic	12	16 to 25
Neotropical	50	120 to 300
Total	352	600 to 965

Where a species is known to occur in more than one region it is allocated, for the purposes of this table, to that most probably inhabited prior to human influence. Minimum figures for the 'probable total number of species' are based on the actual number of species, both described and undescribed, which I have seen from each region. The maximum figures incorporate a fairly generous allowance for, as yet, undiscovered species, derived by extrapolation from other data.

of endemicity within these regions that the majority of species are to be found. For example, in the Neotropical region, large numbers of species occur in Central America and in the northern Andean area, while the *Anotylus* fauna of Chile and Argentina is likely to be very poor, amounting to no more than four species known to me. In continental Asia certain mountainous areas, notably the Himalayas, hills of southern India, and parts of Burma and south-west China, are rich in endemics. Even greater numbers of species are to be found in the islands of Macronesia and the Australasian area, from Sumatra to New Caledonia. In many instances, relatively small islands appear to support endemic species. For example, an estimated 37 species of *Anotylus* (of which some 34 are probably undescribed) were collected during one recent expedition to the Solomon Islands, many of them from no more than a single island in the group.

In common with many other widely distributed staphylinid genera or monophyletic groups of genera, the representation of *Anotylus*, in proportion to area, is not as great in Africa as in other parts of the tropics. However, the mountainous areas of East Africa and Ethiopia are sufficiently rich in endemics that the total number of *Anotylus* to be found in the continent probably exceeds one hundred. As many as fifty species may eventually be found to occur in Madagascar. The faunas of the Palaearctic and Nearctic regions are poor (see Table 1) in comparison with tropical areas, but many species in the northern continents are widely distributed, and it is likely that a comparable number of species are to be found in any one part of these continents and an area of similar size in many lowland continental regions of the tropics.

No truly oceanic island is known to support any endemic species of *Anotylus*, although certain members of the genus have successfully colonized a number of such islands, largely with the aid of human transport (see discussion of 'adventive species' below). Oceanic islands in which *Anotylus* species are known to be recent colonists include St Helena, Tristan da Cunha, Réunion, Seychelles, Mauritius, Norfolk Island, Kermadec Islands, Chatham Islands, Caroline Islands, Mariana Islands, Tahiti and Hawaii. The few species of *Anotylus* known from Madeira, the Canary Islands and the Azores are also likely to be recent immigrants to these islands. However, one or more of the four species known from Iceland (Larsson & Gigja, 1959) are likely to be native. Certain tropical island groups, such as the Galapagos and Aldabra Islands, although fairly well explored entomologically, are not known to support any species of *Anotylus*, native or introduced. It is also noteworthy that the extensive collections of Staphylinidae from many subantarctic and other islands south of about 45° S, which are now available for study, include no *Anotylus* or any other Oxytelinae.

As studies of the taxonomy and phylogeny of *Anotylus* are far from complete, it would be premature to discuss the distribution of monophyletic groups within the genus at any length. However, some general distributional characteristics at this level are already apparent. The rich Neotropical fauna evidently includes a number of endemic species-groups which, apart from (at least) one group which is also represented in the southern parts of the Nearctic, are apparently unrepresented in and cannot be closely associated with the *Anotylus* faunas of other regions.

No trans-Antarctic relationships appear to exist and further study is required before any sister-group relationships between Neotropical and Old World species-groups can be identified. However, some Neotropical groups appear to exhibit close relationships with the New World genus *Apocellus*. Two fairly small and well-defined species-groups are Holarctic in distribution. Other groups represented in the Palaearctic region include species found in other regions of the Old World. The largest of the Palaearctic groups is particularly well represented in Africa, principally in the mountainous areas of Ethiopia and the east of the continent. Although the included species are of sufficiently varied general appearance to have formed the basis of several recently erected genera (Fagel, 1957; etc.), the few species-groups endemic to the Ethiopian region may generally be readily associated with other Old World groups. Several African *Anotylus* belong to species-groups (e.g. the *crassicornis*-group discussed by Hammond (in press)) which are also well represented in Asia, but not elsewhere. The Lemurian *Anotylus* fauna includes many diverse elements, most of them with no evident close relationships elsewhere. A few Madagascan species may be associated with African species-groups and others with groups found in the nearer parts of Asia. However, the nearest extant relatives of certain endemic species or species-groups are likely to be located further afield, possibly in the New Guinea area, or even in the Neotropics. Much further study is needed to elucidate the interrelationships of the many distinct groups to be found in the Oriental-Australasian region, but it is clear that the majority of species-groups are endemic to the region. Evidently the particularly large *Anotylus* faunas to be found in each of the geographical sub-units in the south-eastern part of this area are also composed largely of groups endemic to each respective unit. For example, it is likely that all species of *Anotylus* known from the New Hebrides belong to a single monophyletic group which is confined to these islands. The same may be true of New Caledonia and of most species found in the Solomon Islands, New Britain, New Guinea and the Philippines. Interrelationships between the major monophyletic groups found in this area are evident, as are associations with groups represented in other parts of the Oriental region. However, the large Australian *Anotylus* fauna appears to be, in the main, of independent origin to that of islands to the north and north-east. Most Australian species of the genus belong to a single monophyletic group which, with the exception of one New Guinean species known to me, is confined to Australia. I have so far been unable to detect any close relationships between this Australian group and other species-groups represented in neighbouring parts of the Oriental-Australasian region.

The many resemblances between *Anotylus* and the large genus *Oxytelus*, in range of morphological adaptation, ecological differentiation, etc., naturally prompt comparison of the distributional characteristics exhibited by the two genera. *Oxytelus* is represented by endemic species in all major faunistic regions, including New Zealand (two undescribed species). However, where *Anotylus* is well represented, *Oxytelus* is frequently poorly so, and generally vice versa. This appears to be true not only of representation in geographical areas but also of ecological niches. For example, in south-east Asia most *Oxytelus* are dung-inhabiting species of broad distribution, while the majority of *Anotylus* in the same area are species

of narrow range inhabiting humus or leaf-litter. In Africa, the converse appears to be largely true. Certain lineages within *Anotylus* and *Oxytelus* have converged both morphologically and ecologically, and it is clear that interactions will have influenced the evolution of the two genera and their geographical representation at any given time. Indeed, consideration of the zoogeography and phylogeny of *Oxytelus* may be indispensable in a full discussion of the zoogeography of *Anotylus* and its species-groups.

ADVENTIVE SPECIES

Many of the species of *Anotylus* which inhabit rapidly decaying organic material occupy broad ranges, the extent of which may frequently be due in part to human influence. Most of the widespread species are culture-favoured and able to utilize decaying plant-refuse habitats of the kind created by man in the course of agriculture and other activities, including the dung resulting from animal husbandry. Species of this type which are more or less restricted to but widespread within a single zoogeographical region include *A. clypeonitens* (Pandellé), *A. fairmairei* (Pandellé), *A. imustus* (Gravenhorst), *A. nitidulus* (Gravenhorst), *A. pumilus* (Erichson), *A. sculpturatus* (Gravenhorst), *A. speculifrons* (Kraatz) and *A. tetracarinatus* (Block) in the Palaearctic region, and *A. cognatus* (Sharp) and *A. vicinus* (Sharp) in the eastern Palaearctic-Oriental region. In the Ethiopian region *A. caffer* (Erichson), *A. dilutipennis* (Fauvel), *A. heterocerus* (Fauvel), *A. mirus* (Bernhauer) and *A. stanleyi* (Cameron), and in the Oriental-Australasian region *A. atriceps* (Fauvel), *A. amicus* (Bernhauer), *A. bubalus* (Fauvel), *A. disparatus* (Cameron), *A. hostilis* (Bernhauer), *A. minutus* (Cameron), *A. ocularis* (Fauvel), *A. rubidus* (Cameron) and *A. testaceus* (Motschulsky) fall into the same category. In North America, several species, such as *A. nanus* (Erichson), will probably prove to be widespread. Further taxonomic work is required before other widely distributed elements can be reliably identified in the New World, Australia and elsewhere.

Relatively few species of *Anotylus* appear to have been involved in the kind of faunal exchange which is now well documented for Coleoptera, for example between Europe and North America (Lindroth, 1957). Only such areas as New Zealand and oceanic islands which lack endemic species of the genus have received more than one or two species of *Anotylus* as successful recent colonists. Although relatively few in number, the species of *Anotylus* which have spread, largely by human agency, from one continent to another, are illustrative of a situation which is quite common in the family Staphylinidae as a whole. Truly cosmopolitan species may be lacking in this family, but those which may be classed as subcosmopolitan are likely to exceed one hundred. Although some of these species exploit the dung of domestic mammals, a number, despite the contrary view expressed by Moore & Legner (1974), do not inhabit dung and few are specifically associated with this habitat. Some nine species of *Anotylus* are known to me to be distributed, probably adventitiously, in more than one zoogeographical region. As successful colonists, many of them probably still expanding their ranges, these species are of special interest, and are discussed below. It is hoped that the notes provided will help

to avoid further re-description of these adventive species in regional faunistic works.

A. complanatus (Erichson)

A. complanatus, which is characterized in a number of works dealing with European Staphylinidae (e.g. Lohse, 1964; Palm, 1961), belongs to a species-group with representatives in the Palaearctic region, India and Ethiopia. It is undoubtedly of western Palaearctic origin and today is widespread from Morocco to Scandinavia in the north, and from the Azores to the Caucasus in the east. In northern Europe, including the British Isles, it is almost entirely confined to man-made habitats, and is likely to have extended its original range into these areas and others such as the Atlantic islands as a result of human activity. Although its Palaearctic range and habits suggest that *A. complanatus* exhibits only a slightly greater degree of synanthropy than other widespread species (such as *A. clypeonitens*, etc.) found in the same areas, unlike most other Palaearctic species, it has achieved successful colonization far afield. *A. complanatus* is already known to occur in New Zealand which, as noted above, appears to lack endemic species of *Anotylus*. Specimens which I have seen indicate that *A. complanatus* is probably now common and widespread in that country, and was introduced there, in this case clearly by man, at least one hundred years ago. I have been unable to confirm records of *A. complanatus* for Argentina (Blackwelder, 1944, etc.), but have seen recently collected specimens from Chile (see list of new synonymies above).

A. glareosus (Wollaston)

This species, of undoubted Asian origin, is today almost cosmopolitan in distribution. *A. glareosus* has recently been discussed by Hammond (1975a), who lists countries and regions (including parts of Asia, Africa, Central America, the West Indies, and islands in the Atlantic, Pacific and Indian Oceans) where the species has been found. Diagnoses of the species are provided by Wollaston (1854), Cameron (1930a), Blackwelder (1943) and Hammond (loc. cit.). Although a typical 'island species', *A. glareosus* is neither an inhabitant of dung nor restricted to synanthropic habitats. All other members of the species-group to which *A. glareosus* belongs appear to be inhabitants of forest leaf litter, and are confined to the Oriental region, where they are mostly very locally distributed. Like them, *A. glareosus* is to be found in leaf-litter of primary forests, but also is apparently able to exploit accumulations of vegetable debris in secondary forest or under crop plants. Unusually for a forest litter species it is known to fly to light. Although the spread of *A. glareosus* from Asia has undoubtedly been achieved by means of human agency, perhaps with plants such as bananas, its success as a colonist is probably largely due to intrinsic factors.

A. insignitus (Gravenhorst)

A. insignitus belongs to a Neotropical species-group and is likely to be of Central

American origin. Today it is widespread if not generally distributed within the warmer parts of the New World. I have seen specimens from Brazil, Costa Rica, Mexico, U.S.A., Jamaica, Madeira, Mauritius, Réunion and Tahiti. Records for several other countries and regions in South and Central America and the West Indies are provided by Blackwelder (1944). Although not known to be established in any of the Old World continental land masses, *A. insignitus* is one of the very few Staphylinidae of New World origin to have successfully colonized other regions. The record for France noted by Fauvel (1902) relates to a casual introduction at Marseilles. A useful diagnosis of the species is provided by Blackwelder (1943); the presence of a median clypeal horn will enable the distinction of males from those of other *Anotylus* in most parts of the Old World. Dung of various kinds is the most frequently recorded habitat for *A. insignitus* but specimens have also been taken in compost and heaps of decaying vegetation and, in large numbers, flying to light.

A. latiusculus (Kraatz)

This is the only species of *Anotylus* of undoubted African origin which is known to occur in more than one zoogeographical region. *A. latiusculus* has recently been discussed by Hammond (1975a) who lists the countries and regions where it has been found. It is widespread in Africa and Asia and is also known from Madagascar, Australia and the warmer parts of the Palaearctic region, from Cyprus to Japan. A diagnosis of *A. latiusculus* is provided by Cameron (1930a) and the species is briefly characterized by Hammond (1975a) with the aid of a figure. *A. latiusculus* is apparently strictly confined to dung. Although individuals are frequently taken in flight there are no records relating to specimens procured at light-traps. Its occurrence in some of the most arid parts of southern Africa demonstrate efficient dispersal abilities. However, transport by man may be a relatively unimportant factor in the spread of this species which, unlike many other widespread tropical Staphylinidae, cannot be regarded as an 'island species'.

A. mimulus (Sharp)

Although recorded to date only from Japan this species is likely to be widely distributed in the cooler parts of eastern Asia, as I have seen specimens from northern and eastern China and the Vladivostok area of the U.S.S.R., as well as from a number of Japanese localities. Recently, I have also seen specimens from the U.S.A., taken at Joliet, Illinois, in 1953, and from Chile, taken between 1953 and 1958 in the Santiago district. Transport by human agency is almost certainly responsible for the presence of *A. mimulus* in the New World. A number of other Staphylinidae of eastern Asian origin have spread to other continents during the present century, most notably *Philonthus rectangulus* Sharp, and further spread of *A. mimulus* may be expected if a similar pattern to these species is followed. I have seen specimens of *A. mimulus* taken from the dung of herbivorous mammals and from human excrement. It may also inhabit decaying plant debris. There

are no records to date of its occurrence at light. *A. mimulus* resembles several other Palaearctic species of the 'sculpturatus-group' but may be readily distinguished from other New World species of the genus by a combination of its size - 3 to 4 mm in length, shining black appearance, large puncturation of the fore-parts and, in males, presence of two small tubercles at the posterior margin of the sternite of the 7th abdominal segment.

A. nitidifrons (Wollaston)

This species has recently been discussed by Hammond (1975a) who lists countries and regions where it has been found. Although of undoubted Asian origin it was first described from St Helena. It is now known to occur in parts of Africa, Madagascar and islands in the Atlantic, Indian and Pacific Oceans, as well as in many parts of Asia. It is a typical 'island species', of decidedly synanthropic habits, found in decaying vegetation of various kinds although apparently not in dung; it has frequently been taken at light. Diagnoses of *A. nitidifrons* are provided by Cameron (1930a), Hammond (1975a) and others. Apart from in south-east Asia, where several very similar species are to be found, *A. nitidifrons* may generally be recognized by a combination of the following features: largely yellow colour, head (somewhat variably) darker; shining appearance; absence of reticulate microsculpture from fore-parts; presence of a longitudinal furrow alongside the eye; length 2.8 to 4 mm.

A. pygmaeus (Kraatz)

This species, of probable Asian origin, has recently been discussed by Hammond (1975a). Although further taxonomic work is required before the limits of *A. pygmaeus* may be reliably established, it is clear that it is widespread in the warmer parts of the Old World, as I have seen specimens which I am confident belong to this species from parts of Africa, Madagascar, northern Australia and islands in the Pacific Ocean, as well as from many parts of Asia. This wide distribution is undoubtedly due in part to spread by human agency. *A. pygmaeus* exhibits pronounced synanthropic tendencies and is frequently found in plant refuse heaps, stable manure and human excrement, as well as in more 'natural' accumulations of organic material. Diagnoses of this species are provided by Cameron (1930a) and Hammond (1975a), who also includes a figure. However, as very similar species are to be found in most zoogeographical regions, confident identification requires careful comparison with reliably named specimens of *A. pygmaeus* and other species.

A. rugosus (F.)

This species is characterized in a number of works dealing with European Staphylinidae (e.g. Lohse, 1964), and belongs to a well-defined species-group which, excluding *A. rugosus*, has some 7 Palaearctic and 2 Nearctic representatives. All other

members of this group are much more local and frequently more restricted in habitat than *A. rugosus*, which is very widely distributed in the Palaearctic, from western Europe to the Irkutsk region, and from Italy to the Arctic Circle. It is also widespread in North America; I have seen numerous specimens from many parts of the U.S.A. and Canada, including Newfoundland. Although *A. rugosus* has been regarded by some authors as an inhabitant of dung, compost and similar habitats, it would appear to be typically a species of leaf litter, moss, and vegetable debris in waterside or marshy situations. It is certainly found occasionally in compost but its habits appear to be scarcely synanthropic, and it may be only marginally, if at all, culture-favoured. A naturally broad Palaearctic range is indicated for *A. rugosus*, but the history of its occurrence in North America requires further investigation. I have seen New World specimens dating from about one hundred years ago from several parts of Canada and the U.S.A. As *A. rugosus* is found commonly in Europe north to at least the Arctic Circle and is also known from Iceland (Larsson & Gigja, 1959) it may prove to be one of the very few truly Holarctic species of Oxytelinae. However, introduction by human agency is undoubtedly responsible for the presence of *A. rugosus* in New Zealand. Records indicate that the species was well established in that country at least one hundred years ago, and today is widespread. I have also seen specimens from the (relatively) nearby Chatham Islands. The success of *A. rugosus* as a colonist in New Zealand (and possibly also in North America) is not accounted for by any marked synanthropy. However, in northern Europe it must be regarded as one of the most nearly ubiquitous and generally abundant species of Staphylinidae. The same intrinsic factors may be responsible for both this status and successful recent colonization.

A. vinsoni (Cameron)

Originally described from Mauritius, this species has remained otherwise unrecorded. However, the majority of previous records for *A. sparsus* (Fauvel) are to be referred to *A. vinsoni*. Both species belong to a group which, apart from adventive occurrences of *A. vinsoni*, is restricted to Australia and neighbouring island groups. Scheerpeltz (1935) regarded *A. sparsus* as widespread, and one of the commonest species of 'Oxytelus', over the whole of the Australian continent, New Guinea, Celebes and the eastern Sunda Isles. Fauvel (1903) gives records of *A. sparsus*, in addition, for New Caledonia, Java, Sumatra, Mauritius and Réunion. I have seen specimens of the true *A. sparsus* to date only from the Australian mainland. Most other records for this species are likely to relate to *A. vinsoni*, which I have seen from most of the countries noted above, and also from Hawaii, Tahiti, the Kermadec Islands, Kenya, Tanzania, Cuba and Jamaica. The present almost cosmotropical distribution of *A. vinsoni* is undoubtedly due largely to spread by human agency, probably originally from Australia. Large numbers have been taken flying to light, and the species has otherwise most frequently been recorded from decaying vegetable matter and dung. I have also seen specimens found in cat faeces, tortoise excreta, 'nest debris' and leaf-mould. A diagnosis of *A. vinsoni* (as '*Oxytelus chapini*') is provided by Blackwelder (1943: 101). In Australia

and neighbouring island groups several very similar species are to be found, but elsewhere *A. vinsoni* may be recognized by the following combination of features: length 1.8 to 2.2 mm; fore-parts very smooth and shining, almost completely unsculptured; pronotum yellow, without, or with very weak traces of longitudinal furrows.

Apart from the nine species discussed above several others have clearly extended their original ranges, probably with the aid of human transport, although have not succeeded in colonizing other continents. For example, *Anotylus caffer* (Erichson) occurs on Tristan da Cunha, where it is no doubt a fairly recent immigrant, as well as over a large part of southern Africa. Several species of Australian origin, including *A. brunneipennis* (M'Leay), *A. semirufus* (Fauvel), *A. varius* (Fauvel) and *A. wattensis* (Blackburn), are today found in New Zealand, from whence some of them have been re-described (see list of new synonymies above). One of these, *A. semirufus*, appears to have been particularly successful as a colonist in New Zealand and has also been found on Norfolk Island and the Kermadec Islands.

The ranges of some species of *Anotylus* are likely to be less extensive than reputation currently indicates. The supposedly Holarctic distribution of many species of Staphylinidae frequently derives from instances where New and Old World forms may, in fact, differ specifically. Further study is required before conspecificity of North American populations resembling those of *A. nitidulus* (Gravenhorst) and *A. tetracarinatus* (Block) in the Palaearctic can be predicated with any confidence. However, I have no doubts concerning the conspecificity of Old and New World individuals of *A. rugosus* (F.) but, as noted above, this species may be present in North America as a result of introduction by human agency. Records of *A. tetracarinatus* from Java almost certainly relate to one of several similar Asian species. I have been unable to confirm any extra-Palaearctic records for *A. sculpturatus* (Gravenhorst). Specimens so identified of African origin, which I have examined, all prove to be *A. caffer* (Erichson).

FOSSILS

I have encountered no references to fossil Coleoptera which have been attributed to *Anotylus* but several authors have assigned specimens to *Oxytelus*. Of these, the five listed below have been described as new species.

- Oxytelus proaevus* Heer, 1862 : 45, pl. 3, fig. 5. [Miocene]
- ?*Oxytelus levis* Förster, 1891 : 368, pl. 11, fig. 14. [Middle Oligocene]
- Oxytelus ominosus* Förster, 1891 : 367, pl. 11, fig. 13. [Middle Oligocene]
- Oxytelus subapterus* Wickham, 1913 : 11, pl. 3, fig. 4. [Miocene]
- Oxytelus pristinus* Scudder, 1876 : 79. [Oligocene]

The original descriptions and illustrations pertaining to the first four of these species, are lacking in diagnostic details. However, it is unlikely that they all belong to *Oxytelus* (s. l., including *Anotylus*), or even, in some cases, to the Oxytelinae.

Scudder's original description (1876) of *Oxytelus pristinus* from the Rocky Mountain Tertiaries is suggestive of a modern *Anotylus* of the *rugosus*-group, but without examination of the type, uncertainty regarding the generic placement of this species must remain.

Several species of *Anotylus* have now been identified from late Pleistocene insect assemblages in Europe. Every specimen which I have examined is referable to a known extant species, but two of those found in British Weichselian assemblages demonstrate that striking adjustments of range have occurred during the late Pleistocene. *Anotylus gibbulus* (Eppelsheim) has now been found at several British sites (e.g. Coope, 1970 : 115). Today it is known only from the western Caucasus, and the species-group to which it belongs is otherwise represented only in the Ethiopian region. I have also recently examined *Anotylus* elytra from a British site which are undoubtedly referable to *A. mendus* (Herman), a species which is today found only in a restricted area of eastern Europe, from Austria to south Russia.

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